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CONTENTS

Sanford Myron Zeller ..... HELEN M. GILKEY 357

A nematode-capturing fungus with anastomosing clamp-bearing hyphae ..... CHARLES DRECHSLER 369

Observations on Streptomyces griseus. IV. Induced mutation and strain selection ..... EUGENE L. DULANEY, MYRLE RUGER AND CHARLES HLAVAC 388

The effect of temperature on the papillation of oogonia of Achyla colorata ..... HELEN SIMPSON REISCHER 398

Amino acids in the biosynthesis of Penicillin FREDERICK T. WOLF 403

Chromosome numbers in the Hypocreaceae HILDE E. HIRSCH, WILLIAM C. SNYDER AND H. N. HANSEN 411

An undescribed species of Perioconia C. L. LEFEBVRE, A. G. JOHNSON, AND HELEN S. SHERWIN 416

A cytological study of typical and atypical basidial development in Gymnosporangium clavipes ..... LINDSAY S. OLIVE 420

The taxonomy of Septobasidium Polypodii and S. album J. N. COUCH 427

Oxyporus nobilissimus and the genus Oxyporus in North America ..... WM. B. COOKE 442

Schweinitz-Fries Letters ..... C. L. SHEAR 456

The genus Gomphidius Fries in North America . ROLF SINGER 462

Notes and Brief Articles 490

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SANFORD M. ZELLER, 1885–1948

MYCOLOGIA

OFFICIAL ORGAN OF THE MYCOLOGICAL SOCIETY OF AMERICA

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SANFORD MYRON ZELLER

October 19, 1884–November 4, 1948

HELEN M. GILKEY

Sanford Myron Zeller was born October 19, 1884 in Coldwater, Michigan. Like many another scientist son of a minister, he was born into a home in which culture and education were accepted as a matter of course, and earlier years of schooling naturally led to college.

His interest in science was aroused in high school by a teacher, Miss Burton, whose stimulating presentation and strict discipline in study methods always remained gratefully and affectionately in his memory. After high school he entered Lawrence College in Wisconsin, later transferring to Greenville College in Illinois, which granted him his Bachelor of Science degree in 1909. At the University of Washington in Seattle, where he later became instructor in botany, he obtained the degrees of Bachelor and Master of Arts.

A research fellowship in botany at Washington University, St. Louis, enabled him to receive a Ph.D. at that institution in 1917, where he remained as special investigator in dendropathology until his appointment in 1919 as assistant pathologist on the staff of the Oregon Agricultural Experiment Station at Corvallis. He remained for twenty-nine years of continuous service at this institution, his official title at the time of his death being Plant Pathologist and Professor of Plant Pathological Research.

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During his years at the University of Washington and at the Missouri Botanical Garden, several summers were spent at Friday Harbor Biological Station on Puget Sound, where his main interest was in algae and fungi. That this interest crystallized on the side of fungi rather than algae, seems attributable to two circumstances —one, a visit at that time to the University of Washington by Dr. W. A. Murrill; the other, an incident which occurred one day as Dr. and Mrs. Zeller were rowing on the Sound in search of botanical specimens. Landing in a small cove roofed by an overhanging rock in whose crevices the western maidenhair fern was abundant, they found embedded among the rhizomes numerous glistening clay-colored fruiting bodies of an unknown fungus which later proved to be an undescribed species of *Rhizopogon*. Subsequently it was published under the name *R. diplophloeus* Zeller and Dodge. This new species of a genus which is largely hypogaeous served as his introduction to the intriguing subterranean basidiomycetes upon which he became an undisputed authority. Naturally and necessarily his interest widened to cover the entire field of Gasteromycetes, of which a contemporary internationally known mycologist writes, "He had, in my estimation, the best first-hand knowledge of the group as a whole of any man in the United States or Canada. And he was a world-recognized authority." Another mycologist, likewise world-known, states, "In his chosen field, the Gasteromycetes, Dr. Zeller was first among living authorities. The better-known groups, like the puffballs and phalloids, have been admirably treated a number of times. But the field studies which were made possible by the riches of his own Northwest, and the painstaking investigation of odd or imperfectly understood forms from elsewhere, made his knowledge unique. In a day when most of us are happy to be able to claim aquaintance merely with one or another *-aceae* he was that rare and heartwarming phenomenon, a Good Mycologist."

In spite of his attainments in this field, the Gasteromycetes represented, of necessity, a side-issue professionally, for by appointment he was a plant pathologist and in constant touch with the need for pathological research in the Northwest. During his twenty-nine years in Oregon, he assisted in solving many knotty problems relating particularly to berry and tree-fruit production in the state.

A glance at the appended list of his publications will suffice to indicate somewhat the variety of problems involved and the value, to the fruit-growers and farmers, of his investigations. Strawberries and cane-fruits, pomaceous and drupaceous tree-fruits, all came in for their share of attention; and Northwestern orchards are cleaner and more profitable because of his work and that of his associates. But his interest in pathology was not confined to crop plants. Any leaf-spot or other indication of disease caught his eye, and required of him an investigation into its life history. Note, for instance, such items as: "New or noteworthy fungi on Ericaceous hosts in the Pacific Northwest"; "An anthracnose of *Ledum*"; "A witches' broom of Ocean Spray."

More than one hundred fifty scientific papers were prepared for publication by Dr. Zeller, alone or in collaboration with other authors, most of the subjects relating to fungi. Outstanding among these are his contributions to a knowledge of the Gasteromycetes. The following mathematical data are more than mere figures, for into them can be read something of Dr. Zeller's familiarity with the fields in which he worked, his persistent and consistent application to research in spite of difficulties, and his scientific curiosity which gave him no rest. Independently he described three new orders, nine families, six genera, eighty-one species; and established twenty-nine new names and combinations. Added to these are three new genera, sixty-two species, and fifty-nine combinations published in co-operation with other scientists.

During his last year, he spent a four months' sabbatical leave at the New York Botanical Garden, preparing the comprehensive treatment of the Gasteromycetes which had been requested of him for inclusion in the North American Flora. Fortunately he was privileged to complete considerable of the manuscript, particularly the very important keys whose publication has given to mycologists one of his conspicuously important contributions to science.

The hypogaei were perhaps his best love. Always in his car he carried a short-handled rake, and he was rarely known to pass a likely piece of woods without stopping to do a little tentative grubbing. He was one of those rare collectors of these elusive fungi who never came away empty-handed. The ability to discover subterranean fungi involves principally three characteristics

—an understanding of their requirements, good judgment in applying this understanding, and luck. The order and proportions of these three factors are not fixed, and many an unsuccessful grubber would like to believe that the third is paramount. Whatever the case, Dr. Zeller invariably brought home a handful or two of fruiting bodies—not only of his own group but also, frequently, of those hypogaeous ascomycetes, the Tuberales, generally much rarer.

Concerning his collecting of subterranean fungi, Dr. Zeller always had a new good story on himself. On one occasion he, with a party of other enthusiastic collectors ("groundhoggers" was the official name), thoroughly worked over a mixed grove of conifers and deciduous shrubbery. When they had finished, it must be admitted that with the moss rolled back and the duff in large quantities removed from beneath the trees, the woods looked considerably worse for wear and certainly must have been perplexing to any passing layman. Having occasion, in line with his duties as pathologist, to visit fruit-growers in the vicinity sometime later, he was startled to be informed of a recent cougar hunt organized by the farmers of the community. His surprised exclamation brought the reply, "Yes, sir, a few weeks ago we found the grove yonder all clawed up, and nothing smaller than a cougar could have done it. So we all went out for a day with our guns—but the critter's still at large." When Dr. Zeller recounted the story and his friends asked, superfluously, whether he had enlightened the farmers, his deep chuckle was sufficient answer to the foolish question.

Dr. Zeller was a member of the American Mycological Society, of which last fall he was elected vice-president; of the Phytopathological Society of whose Pacific Division he was president from 1922 to '24, and a member of its advisory board from 1925 to '28. He was associate editor of its official organ, *Phytopathology*, from 1924 to '30; was a member of Alpha Sigma Delta; and was elected to honorary membership in Phi Sigma. On the Oregon State College campus he served for a year as president of the local chapter of the Sigma Xi; a year as president of the Phi Kappa Phi chapter, and was its delegate to the national convention in 1933. In 1913 he was a member of the Alaska kelp expedition conducted by the Bureau of Soils, U.S.D.A.

Though his professional responsibilities and accomplishments would appear to require a full-time schedule, he somehow found time for other important activities. A member of the official board of the local Methodist church, he helped carry through the construction of the impressive present building of that denomination; and for twenty-two years he was chairman of the advisory committee of Wesley Foundation, which has done outstanding service for college young people. Special honors were to have been accorded him at the twenty-fifth anniversary of this student group, but the date fell upon the day following his death.

With four daughters in the family, Dr. and Mrs. Zeller for years were actively interested in Camp Fire; and were so largely responsible for the effective organization and smoothly-running machinery of the Corvallis Council that in 1948 they were each granted the Luther Gulick award given volunteer workers for extraordinary service.

Properly to appraise Dr. Zeller's contributions to science and to the community, one must know that stalking all his activities was the illness which had followed him from childhood, had weakened his otherwise powerfully-built frame, and from which he never was completely free. He treated it casually; if he ever complained, no one knew it. "Patient through suffering" is the thought which now comes to his friends far more frequently than when he seemed naturally to hold his place among individuals of normal health. The sympathetic understanding and co-operation in his home and the companionship of his friends were of fundamental value to him. He will be missed as a scientist. Even more he will be missed by those who knew the twinkle of his eye, his ever-ready story, his deep infectious laugh, and the kindness of his heart.

OREGON STATE COLLEGE,
CORVALLIS, OREGON

LIST OF PUBLICATIONS BY S. M. ZELLER OR IN JOINT AUTHORSHIP

1. The development of *Stropharia ambigua*. Mycologia **6**: 139–145. *Illus.* 1914.
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3. (With T. C. Frye) *Hormiscia tetraciliata* sp. nov. Puget Sound Biol. Sta. Publ. **1**: 9–13. *Illus.* 1915.
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6. Studies in the physiology of the fungi. II. *Lenzites sacpiaria* Fries, with special reference to enzyme activity. Ann. Mo. Bot. Gard. **3**: 439–512. *Illus.* 1916.
7. *Idem.* III. Physical properties of wood in relation to decay induced by *Lenzites sacpiaria* Fries. *Ibid.* **4**: 93–164. *Illus.* 1917.
   (Above reprinted *in toto* as American Railway Engineering Association Bul. **198** (Vol. 19): 6–60. *Illus.* 1917).
8. (With C. W. Dodge) Rhizopogon in North America. Ann. Mo. Bot. Gard. **5**: 1–36. 1918.
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65. (With E. K. Vaughan) Crinkle disease of strawberry. *Ibid.* **22**: 709–713. *Illus.* 1932.
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104. (With S. C. Jones, C. E. Owens & R. H. Robinson) Tentative program for the control of sour-cherry leaf-spot, Syneta beetle, and fruit fly in 1941. Ore. Agr. Exp. Sta. Mimeo. Cir. Info. No. 225. *Illus.* December 1940.
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110. (With Arlyn W. Evans) Transmission of western X-disease and marginal leaf-spot of peach in Oregon. Plant Dis. Reporter **25**: 451–453. 1941.
111. (With C. E. Owens & A. W. Evans) Experiments on the control of cherry leaf-spot, 1939–1941. Ore. State Hort. Soc. Ann. Rept. **33**: 56–58. December 1941.
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114. (With L. E. Weaver) Stunt disease of strawberry. Phytopath. **31**: 849–851. *Illus.* 1941.
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118. (With C. B. Cordy) Buckskin disease of cherry in Southern Oregon. Plant Disease Reporter **26**: 141. 1942.

119. (With J. A. Milbrath) Sycamore leaf- and twig-blight (anthracnose). Ore. Agr. Exp. Sta. Mimeo. Cir. Info. No. 270. 1942. (Revision of Cir. No. 38, 1930.)
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A NEMATODE-CAPTURING FUNGUS WITH ANASTOMOSING CLAMP-BEARING HYPHAE

CHARLES DRECHSLER[1]

(WITH 4 FIGURES)

Under the genus *Nematoctonus* I have described earlier five nematode-destroying fungi whose hyphae are liberally beset with clamp-connections of the kind long known as being characteristic of some groups in the Basidiomycetes. Four of these fungi, namely *N. tylosporus* (**1**), *N. leiosporus* (**1**), *N. pachysporus* (**3**), and *N. leptosporus* (**3**), attack in a rather commonplace parasitic manner by sending a germ tube into the animal host from an externally adhering conidium. Necessarily the conidium in these parasites, and, indeed, in the generality of fungous parasites subsisting on free-living terricolous nematodes, must adhere very firmly, for otherwise it would almost certainly be dislodged as the animal continues to move briskly through materials of close texture during the period required for penetration of the integument and slow transfer of spore contents into the invading hyphal tip. In *N. tylosporus* and *N. leptosporus* the conidium secretes a minute mass of glutinous material at its apex while it is still supported on its sterigma. However in these two species, as also in *N. leiosporus* and *N. pachysporus*, the adhesive organ most usually found operating effectively is formed after the spore has become detached, the fallen conidium then regularly putting forth a short, erect or ascending outgrowth with a glandular tip, or terminal glandular cell, that secretes a sizable globule of adhesive material. In *N. haptocladus* (**4**), the fifth member of the genus to be named and described, similar adhesive outgrowths or adhesive organs are formed

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not only on fallen conidia, but also on the vegetative mycelium, usually being produced distally on prostrate hyphal branches as upcurving terminations. Rather often, especially when the proximal filamentous connection has been weakened through withdrawal of protoplasmic contents, the specialized hyphal termination is torn loose by a vigorous adhering eelworm, and then is carried away by the doomed animal much like a fallen conidium with glutinous outgrowth. Yet often, again, the hyphal connection withstands the struggles of the adhering eelworm, which consequently is held captive while undergoing invasion and, after death, expropriation of its fleshy substance. In view of the predacious manner of attack thus revealed, *N. haptocladus* offers an engaging parallelism with the few nematode-capturing phycomycetous forms found among the Zoopagaceae, as well as with the considerably more numerous nematode-capturing species that have been made known in the series of clampless predacious hyphomycetes.

Another species of *Nematoctonus* that attacks free-living terricolous eelworms both parasitically and predatorily came to light more recently in several maizemeal-agar cultures, which, after being overgrown with uncontaminated mycelium of *Pythium irregulare* Buism., had been further planted with pinches of decaying chess (*Bromus secalinus* L.) detritus taken from a handful of this material kindly gathered by Dr. W. J. Zaumeyer near Hermiston, Oregon, on August 20, 1947. The new *Nematoctonus* usually made its appearance ten to fifteen days after the addition of the decaying residues and in all instances obviously subsisted altogether on the many eelworms that soon had infested the cultures. Nearly all of the eelworms present belonged either to a somewhat robust species kindly identified by Dr. G. Steiner as *Panagrolaimus subelongatus* Cobb, or to a much more slender species determined as *Ditylenchus* sp. The two types of nematodes were utilized by the fungus without evident preference, though owing to its much greater abundance *P. subelongatus* was destroyed in larger numbers.

Unlike *Nematoctonus haptocladus*, which often is first observed developing in agar plate cultures at some distance from the decaying materials whence it originates, the Oregon fungus regularly begins its visible development in tracts bordering the planted detritus, and then spreads progressively into more remote areas.

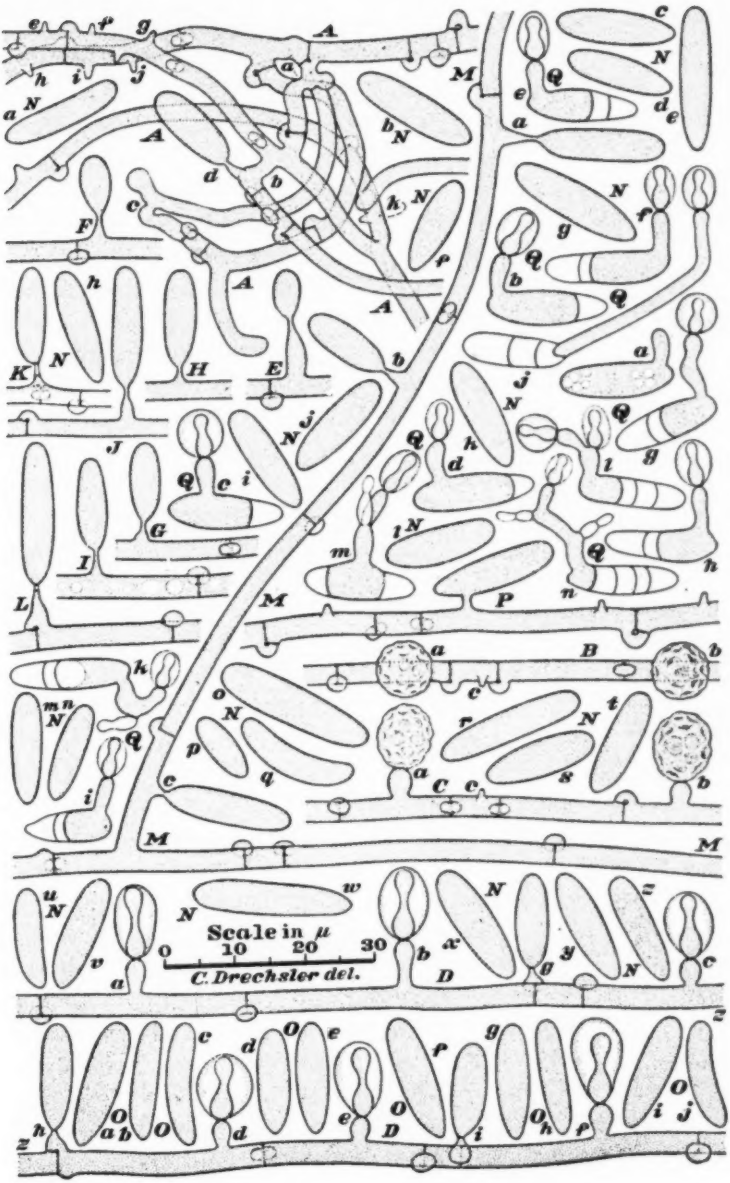

FIG. 1. *Nematoctonus concurrens.*

Nevertheless its ramifying mycelium (FIG. 1, *A*) greatly resembles that of *N. haptocladus* in general aspect, the constituent hyphae (FIG. 2, *A, a, b; B, a, b.* FIG. 3, *A; J, a, b; K, a–c.* FIG. 4, *A; B, a–c*) being filled while in their youthful condition with protoplasm of nearly homogeneous consistency. The longer filaments are little given to abrupt changes either in width or in direction. All mycelial elements except the shortest branches are studded with clamp-connections. For the most part the clamps are spaced at distances of 20 to 80 μ, but here and there they are wont to occur in more crowded arrangement with some intervals not exceeding 2 μ. Apparently no cross-walls other than those associated with clamp-connections are formed to serve as ordinary partitions between adjacent living undifferentiated vegetative hyphal segments. Hyphal fusions (FIG. 1, *A, a–c.* FIG. 2, *A, c, d; B, c, d.* FIG. 3, *A, a; I, a; J, c; K, d, e.* FIG. 4, *A, a–c; B, d*), which have not been observed either in *N. haptocladus* or in any of the four congeneric parasites, occur here in sufficient numbers to be immediately noticed, though scarcely with the frequency of anastomoses in the clampless nematode-capturing hyphomycetes.

The mycelium of the Oregon fungus, like that of *Nematoctonus haptocladus*, is furnished with predacious organs consisting individually of a globose adhesive body borne aloft 2 to 7 μ above the substratum on a short stalk rising vertically from a prostrate hypha. When examined microscopically from above, in their undisturbed posture and without any addition of water, they appear as projecting knobs with a pitted or irregularly indented surface (FIG. 1, *B, a, b;* FIG. 2, *A, e–o;* FIG. 4, *A, d*); their internal make-up and underlying hyphal connections being then only indistinctly visible or sometimes even wholly obscured. Viewed from the side in a dry mount the hyphal connections stand out clearly, but the internal make-up of the adhesive body still remains concealed (FIG. 1, *C, a, b*). The composition of the predacious organ is seen better in material that has been slightly moistened and with gentle pressure covered with a cover glass; the adhesive body in material thus mounted presenting a smoothly rounded profile, and revealing within it an elongated cell conspicuously narrowed in the equatorial region somewhat after the manner of an hour-glass (FIG. 1, *D, a–f.* FIG. 2, *B, e–o; C, a, b; D, a, b; E, a–c; F, a–c; G, a–f; H, a; I, a–c; J, a;*

K, a; L, a–c; M, a. FIG. 3, *A, b; B, a, b; C, a, b; D, a, b; E, a; F, a; G, a, b; H, a, b; I, b, c; J, d–f; K, f–h.* FIG. 4, *B, e–h; C, a*). A very distinct line of demarcation always separates the distally rounded protuberant stalk from the proximally rounded elongated cell. Although an abrupt junction of two rounded lobes might in itself be expected to offer much the appearance of a septum even where no septum exists, close examination of many predacious organs has inclined me strongly to the belief that a delimiting cross-wall is really present here—this cross-wall, of course, being an ordinary one, not associated with a clamp-connection.

Near its attachment to the stalk for a distance upward of about 1.5 μ, the peripheral wall of the elongated cell seems slightly thickened and has a somewhat dark indurated appearance. Beyond this more substantial collar-like part the envelope is uniformly thin, though yet of sufficient thickness to remain clearly visible throughout; the fungus thereby differing from *Nematoctonus haptocladus*, in which the membrane of the corresponding cell is so thin at the rounded distal end as to be virtually indiscernible. It may be presumed that whereas in *Nematoctonus haptocladus* the glutinous substance surrounding the cell is probably given out mainly from the very thin-walled apical region, exudation in the Oregon fungus may take place about equally from all portions of the membranous envelope above the indurated collar-like part. The glandular cell of the Oregon fungus is fully twice as long as that of *N. haptocladus*, and, in general, about half again as wide. Its narrower shape is accentuated in some degree by its more gradual and more extended median constriction. Its greater volume and dimensions are reflected in correspondingly greater volume and dimensions of the globule of adhesive material secreted by it; and its more elongate form seems associated with a noticeably greater tendency toward an elongated shape in the globule.

Some protuberant stalks after producing a glandular cell in the usual way will grow out laterally or obliquely at the tip and give rise on a short prolongation to a second glandular cell (FIG. 3, *J, g*). The process may be repeated again with the resulting development of a third glandular cell (FIG. 2, *H, b*). Such successive development, like the similar development noted earlier in *Nematoctonus haptocladus* as well as in *N. pachysporus*, is frequently preceded by

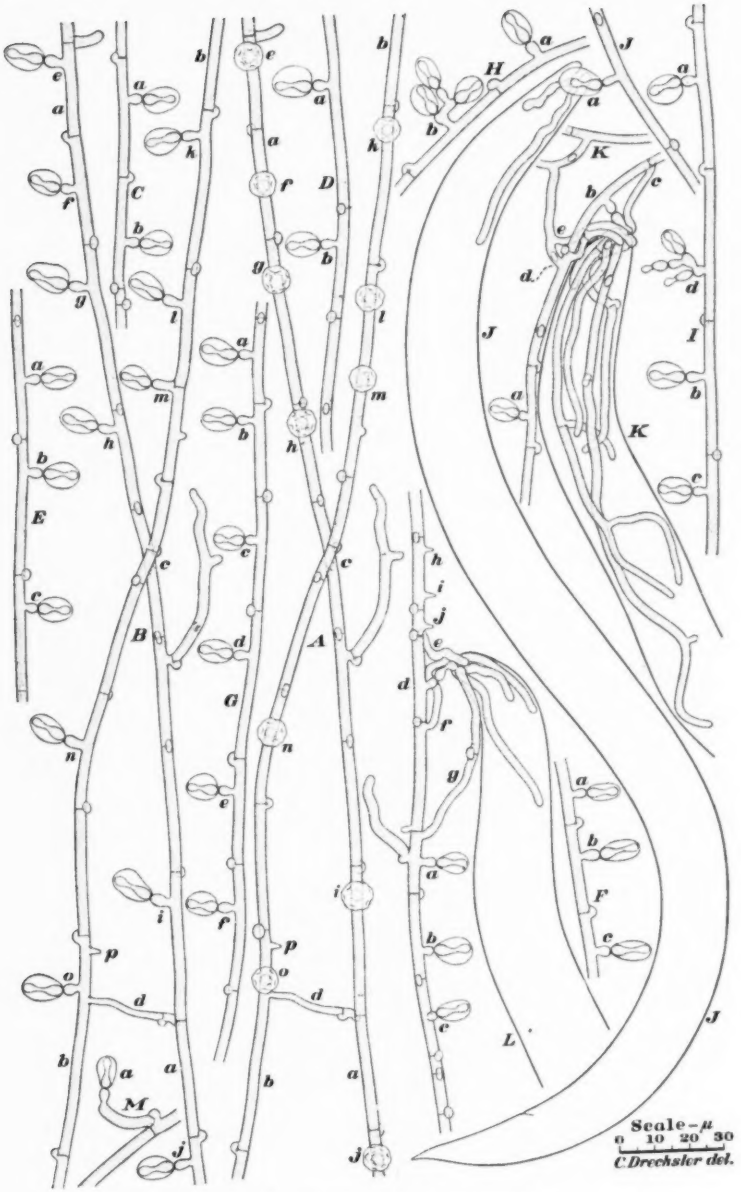

FIG. 2. *Nematoctonus concurrens.*

degeneration in the older glandular cells—this degeneration becoming manifest usually in withdrawal of protoplasmic contents from the distal lobe (FIG. 3, *J, h*), together sometimes with disappearance of the enveloping mass of adhesive material (FIG. 2, *I, d*). In instances where the distal lobe is found empty while the proximal lobe is still filled with protoplasm, the retaining wall present in the constriction consists of an ordinary partition not associated with a clamp-connection.

As the very short erect stalks supporting the glandular cells always arise from prostrate hyphae, never being borne on submerged or ascending mycelial filaments, the Oregon fungus, much like *Nematoctonus pachysporus,* is capable of capturing only nematodes moving on the surface of a culture. In its usually forward movement, the animal commonly strikes the raised adhesive globule with the anterior portion of its body, often, indeed, being found held directly by its head (FIG. 2, *J, a.* FIG. 3, *I, b, c; J, i; K, i.* FIG. 4, *B, i; D–G: a; H, a*); though attachment to adhesive organs also takes place farther backward (FIG. 4, *B, j, k*). Adhesion to a single predacious organ suffices, as a rule, for the capture of robust specimens of either *Panagrolaimus subelongatus* or *Ditylenchus* sp. After the struggles of the captive have diminished in violence, presumably from exhaustion, the glandular cell puts forth a narrow process which perforates the animal's integument, then immediately widens out and begins growing through the fleshy interior as an assimilative hypha (FIG. 3, *H, c;* FIG. 4, *D, a*). In many instances the assimilative hypha soon gives off a branch close to its origin (FIG. 2, *J, a;* FIG. 4, *H, a*), but often, again, it may attain a length of approximately 100 μ while remaining in a simple condition (FIG. 3, *I, b, c; J, i.* FIG. 4, *E–G: a*). Branching in assimilative hyphae frequently is accompanied, or perhaps rather closely followed, by the formation of clamp-connections (FIG. 2, *K, b;* FIG. 3, *K, i*).

Although a single predacious organ usually is altogether effective in holding fast a moderately robust eelworm, the struggling animal often brushes against other predacious organs, and thus becomes affixed in two (FIG. 3, *H, b, c; I, b, c*), three (FIG. 4, *B, i–k*), or more places. Since here, as in nematode-capturing fungi generally, each predacious organ operates rather independently of others, captives often incur multiple invasion by reason only of their multiple

affixture (FIG. 3, *I, b, c*). In the Oregon fungus multiple infection further comes about very frequently through the curious development of accessory infective branches (FIG. 2, *K, c–e; L, e–g.* FIG. 3, *I, d; J, j–l; K, j–m.* FIG. 4, *B, l, m; C, c; D–G: b, c; H, c*). These branches arise usually at distances of 10 to 50 μ from a predacious organ that has newly captured a nematode. Very often they are put forth from the same hypha that bears the predacious organ (FIG. 2, *K, c, d; L, e–g.* FIG. 3, *J, l.* FIG. 4, *B, l; C, c; D, b, c*), but with about equal frequency they originate from neighboring hyphae, which in some instances have an observable connection with the predacious organ either from the ramification of the mycelium (FIG. 2, *K, e*) or from anastomosis of mycelial filaments (FIG. 3, *K, j–m*), but in other instances lack such connection (FIG. 3, *J, j, k;* FIG. 4, *B, m*). Often the growth of the accessory branches is from the beginning rather accurately directed toward the position where the struggling animal is held fast by the fungus (FIG. 3, *J, l;* FIG. 4, *D, b*), though often, again, their courses seem rather haphazard or even circuitous (FIG. 4, *B, j; D, c*). Despite some aberration they converge unmistakably as they elongate (FIG. 4, *E, b, c*), and after about an hour or perhaps two hours of growth they reach their goal, each bringing its tip against the animal's integument in immediate proximity to the adhering predacious organ (FIG. 4, *B, l, m; F, b, c*). On penetrating the integument the individual branch intrudes a prolongation which then extends itself autonomously through the fleshy interior as an assimilative hypha (FIG. 4, *C, c; F, b; G, b*) in fellowship with the assimilative hypha arising from the predacious organ.

Although in most cases the number of accessory infective branches associated with a predacious organ ranges from one to five, development of such branches in numbers from six to ten occurs rather often, and instances of development in numbers from eleven to fifteen come under observation at least occasionally. The convergence of multiple branches makes for an appearance strongly reminiscent of sexual reproductive apparatus in species of oomycetes where the oogonium is fertilized by plural antheridia. No development of accessory infective branches was recorded in my account of *Nematoctonus haptocladus* or in the descriptions of the four congeneric species, though until further observations are made

the possibility is not to be dismissed that among these closely related forms similar development might occur on so small a scale as readily to escape detection. The accessory infective branches produced by the Oregon fungus offer some little resemblance to the supplementary connections formed in some clampless nematode-capturing hyphomycete species—my *Dactylella doedycoides* and my *D. heterospora* (**2**: 341–342) may be cited as examples—where the stalk supporting the predacious organ lacks sturdiness, owing mainly to its length, and consequently often suffers injury from the struggles of the prey. These supplementary connections, however, are commonly produced only singly and, as a rule, are intercalated between two fungus cells external to the animal. Unlike the accessory infective branches, they generally neither penetrate the animal's integument anew nor intrude an additional assimilative hyphal system; their function evidently being only to supply better communication between the external mycelium and the assimilative hyphae intruded by the predacious organ.

Since in most instances a captured specimen of *Panagrolaimus subelongatus* adheres to the predacious organ by its head, invasion of its body proceeds commonly from the head (FIG. 2, *J–L;* FIG. 3, *I–K;* FIG. 4, *D–G, H*) toward the tail. The angular relationships of the ramified mycelium in the posterior portion of a dead captive (FIG. 3, *L;* FIG. 4, *I, J*) suggest strongly that hyphal fusions must occur rather frequently among assimilative filaments, even though it is true that an appearance of hyphal fusion is often simulated here through the circumstance that many branches are extended in a direction opposite to the direction of growth of the parent filament. As a rule the protoplasm elaborated by the fungus from the contents of a relatively small eelworm is transferred to the external mycelium entirely through the adhesive organ and accessory infective branches. This is often true also where larger animals are concerned, if many accessory infective branches are present. However, in many instances where the eelworm is of large size and only a few accessory infective branches are present, a portion of the elaborated protoplasm is used in extending several hyphae—often about five or six—out from the posterior (FIG. 3, *L, a, b;* FIG. 4, *J*) and median portions of the animal. Obviously these erumpent hyphae belong with the

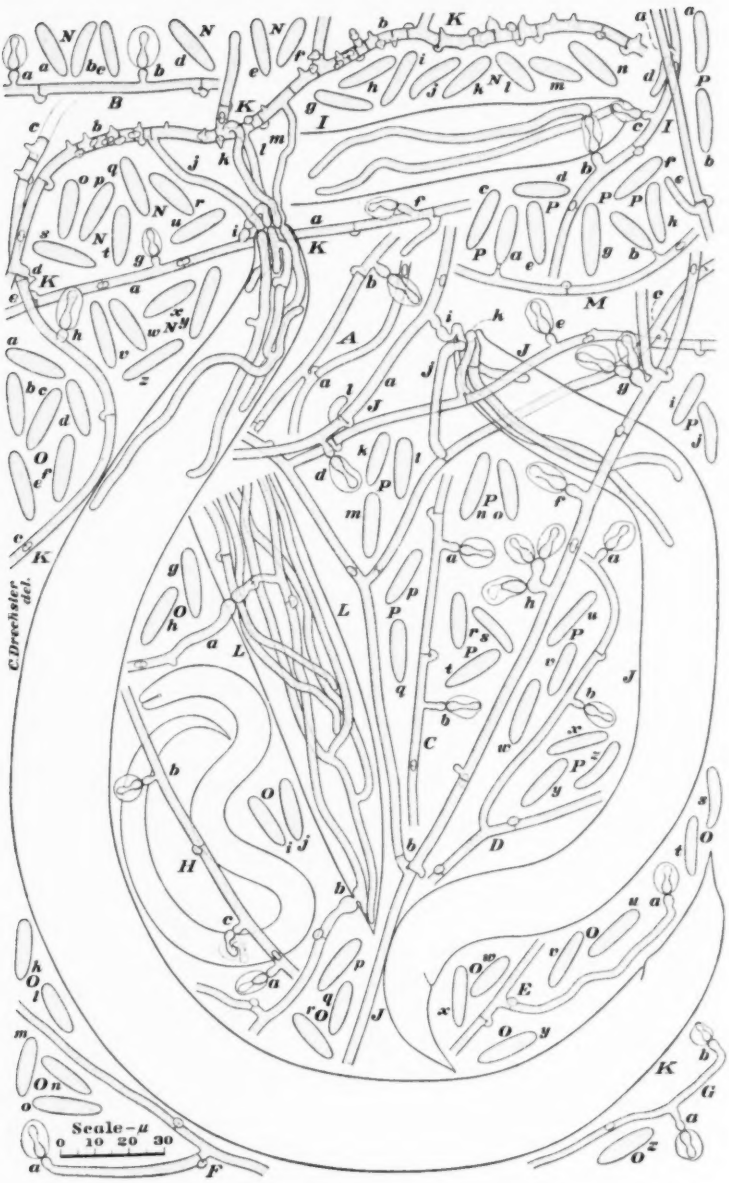

FIG. 3. *Nematoctonus concurrens.*

external mycelium, and therefore, after some elongation and branching, may put forth predacious organs and conidia.

In contrast to *Nematoctonus haptocladus*, which produces conidia only rather sparingly, the Oregon fungus usually shows abundant sporulation. Its prostrate mycelium gives rise to conidia haphazardly (FIG. 1, *A, d–k*), the longer procumbent hyphae often bearing them (FIG. 1, *D, g–i;* FIG. 2, *A, p;* L, *h–j*) interspersed among predacious organs. They originate as terminal swellings on tapering sterigmata (FIG. 1, *E, F*) and increase in size with continued accession of protoplasm from below (FIG. 1, *A, d; G–J*) until they become delimited from the slender supporting tip by a septum (FIG. 1, *K, L;* FIG. 4, *K*). On the ascending hyphae, which regularly are devoid of predacious organs, conidia are produced in the beginning at rather wide intervals (FIG. 1, *M, a–c;* FIG. 3, *M, a, b*), but seemingly more conidia are later put forth from intercalary positions, to provide eventually a bristling display (FIG. 4, *L, M*). Prostrate (FIG. 3, *K, b, c*) as well as aerial (FIG. 4, *N–P*) hyphae on which conidia have been produced at close intervals show in their denuded condition a conspicuously close arrangement also of clamp-connections.

Although slightly plumper and appreciably larger, the mature detached conidia of the Oregon fungus (FIG. 1, *N, a–z; O, a–j.* FIG. 3, *N–P: a–z.* FIG. 4, *Q, a–z*) most nearly resemble, among congeneric forms, those of *Nematoctonus haptocladus* with respect to size and shape. In my cultures they germinated less freely than the conidia of *N. haptocladus*, but their germinative development followed essentially the same course. The fallen spore would first send up a short erect outgrowth from a position usually near one of its ends, as simultaneously several clustered vacuoles came into view toward its other end (FIG. 1, *Q, a*). On the rounded tip of the spur-like outgrowth a glandular cell, noticeably smaller but otherwise similar to glandular cells of mycelial origin, was then produced while the farther end of the spore was emptied of protoplasmic contents with concomitant formation of one (FIG. 1, *Q, b–d*) or two (FIG. 1, *Q, e–i*) retaining walls. In one observed instance (FIG. 1, *Q, j*) the spore envelope was almost wholly emptied from production of a single glandular cell at the tip of a germinative outgrowth over 30 μ long—this being fully six times the usual length

of the erect support. Ordinarily, however, about one-half to three-fifths of the protoplasm was left over, so that the conidium through further withdrawal of contents (FIG. 1, *Q, k*) and deposition frequently of a third retaining wall (FIG. 1, *Q, l*) was capable of giving rise to a second glandular cell on a short prolongation of the germinative outgrowth. Occasionally a conidium that had produced a second glandular cell on an outgrowth arising from a median position showed an empty segment at each end (FIG. 1, *Q, m*). Following the degeneration of the first two glandular cells produced by them some conidia extended their outgrowth again to form a third glandular cell (FIG. 1, *Q, n*), thereby emptying a fourth segment though yet retaining about one-fifth of their original protoplasmic contents—enough, presumably, to have made possible the formation later of a fourth glandular cell.

Each glandular cell produced on a germinative outgrowth soon secretes an enveloping globule of adhesive material which serves, whenever opportunity offers, to attach the conidium to some roving eelworm (FIG. 4, *H,'b*). An animal that has been thus encumbered may continue to move about until it is disabled from progressive invasion by an assimilative hypha intruded by the adhering spore, but rather often before such disablement supervenes it encounters a predacious organ and is held fast (FIG. 4, *H, a*). In the latter event the glandular cell produced by the conidium may evoke development of accessory infective branches (FIG. 4, *H, c*) after the same manner as glandular cells of mycelial origin. As the very numerous conidia in my cultures gave rise to adhesive outgrowths only sparingly, the Oregon fungus displayed little of the strong capabilities for parasitic attack it assuredly should unfold under conditions favorable for germination of its spores. Owing to the enduringly sturdy attachment of its predacious organs, including those borne on lateral branches (FIG. 2, *M, a;* FIG. 3, *F, a; G, a, b*), it affords little scope for the simulation of parasitic attack usual in *Nematoctonus haptocladus,* where the attachment of predacious organs often becomes weakened early through evacuation of the proximal segments of the branches on which they are borne.

Occasionally a fallen conidium is found united to a neighboring mycelial filament by means of a short hyphal connection (FIG. 1, *P*). Manifestly such a fusion is of the same character as the hyphal

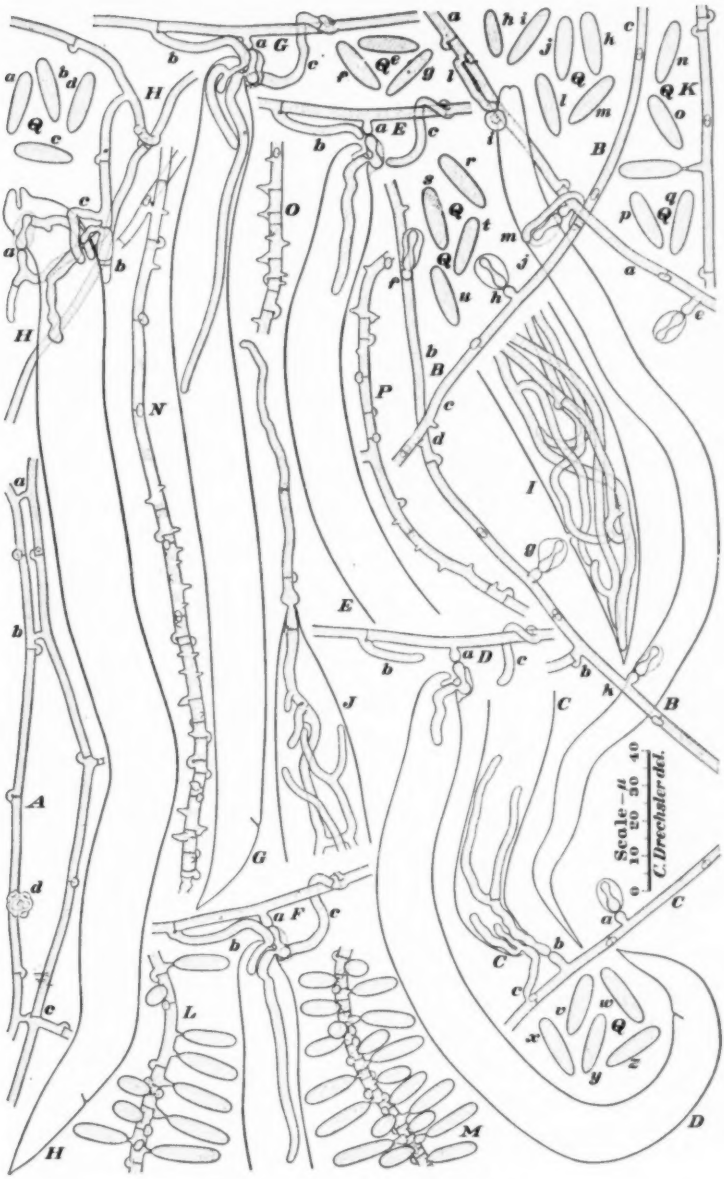

FIG. 4. *Nematoctonus concurrens.*

anastomoses so frequent in the fungus, and like these offers parallelism with the clampless nematode-capturing hyphomycetes. Since hyphal fusions serve to join numerous small mycelia into more extensive three-dimensional tracts, and in some basidiomycetes bring about nuclear relationships necessary for sexual development, the Oregon fungus would seem, perhaps somewhat more likely than the several congeneric forms previously described, to yield a basidial stage visible to the naked eye. In my cultures, however, no basidial stage ever came to light, nor was any reproductive apparatus ever found produced by the fungus apart from the conidial apparatus herein discussed. The fungus is therefore described in the genus *Nematoctonus*, and under a specific epithet having reference to the convergence of its accessory infective branches.

Nematoctonus concurrens sp. nov.

Mycelium tenellum, oculo nudo parum visibile, aliquid araneosum. Hyphae procumbentes incoloratae, filiformes, ramosae, in modum Hymenomycetum septato-nodosae, saepe inter se conjunctae, 2–3.5 μ crassae, cellulas glutinosas in apice columellarum atque conidia in apice sterigmatum gignentes; his columellis erectis, plerumque 3–7 μ altis, basi circa 2 μ crassis, sursum 2.4–3.7 μ crassis, apice rotundis; cellulis glutinosis harum 6–12 μ (saepius circa 10 μ) longis, 2.5–4 μ crassis, medio gradatim sed valde constrictis itaque ibi modo 0.8–1.5 μ crassis, primo nudis sed mox pila glutinis globosa vel ellipsoidea 6–12.5 μ longa, 4–8.5 μ crassa circumdatis, denique saepe ad vermiculum nematoideum inhaerentibus, itaque animal capientibus, cuticulam ejus perforantibus, quandoque tantummodo ipsis quandoque cum 1–15 ramulis adjunctis 10–50 μ longis hyphas assumentes incoloratas ramosas septato-nodosas intrudentibus quae carnem exhauriunt et interdum ramos mycelii extra emittunt. Hyphae ascendentes incoloratae, parce ramosae, septato-nodosae, 2–3.5 μ crassae, conidia in apice sterigmatum ferentes; sterigmatibus interdum ex nodis oriundis, 1.8–7 μ longis, basi 1.2–2.5 μ latis, sursum attenuatis, apice 0.6–0.8 μ latis. Conidia incolorata, cylindracea vel elongato-ellipsoidea, recta vel leniter curvata, sursum late rotundata deorsum similia vel leviter attenuata, plerumque 10–23 μ longa, 3.6–5.6 μ crassa, primo continua et protoplasmatis omnino repleta, post disjunctione ex apice columellae germinationis cellulam glutinosam ferentia, deinde quandoque identidem prope apicem columellae recrescentia 1 vel 2 alias cellulas glutinosas gignentia, denique in magna parte vel omnino inania et 1–4 septis intus divisa; cellulis glutinosis germinationis 4.5–6.5 μ longis, 2–2.5 μ crassis, medio constrictis, pila glutinis globosa vel ellipsoidea 4–7 μ longa 3.5–6.5 μ crassa mox vestitis.

Panagrolaimum subelongatum et *Ditylenchum* sp. capiens consumensque habitat in foliis caulibusque Bromi secalini putrescentibus prope Hermiston, Oregon.

Mycelium delicate, arachnoid, faintly visible to the naked eye. Prostrate hyphae colorless, filamentous, branched, 2 to 3.5 μ wide, studded with clamp-connections and often joined to one another by anastomosing connections, at variable intervals giving rise on protuberant outgrowths to glandular cells and producing conidia on the tips of sterigmata; the protuberant outgrowths regularly erect, mostly 3 to 7 μ high, about 2 μ wide at the base and 2.4 to 3.7 μ wide toward the rounded tip; the glandular cells here 6 to 12 μ (usually about 10 μ) long, 2.5 to 4 μ wide, gradually but strongly constricted at the middle and thus measuring only 0.8 to 1.5 μ in that region, at first naked but later always surrounded by a globose or ellipsoidal mass of glutinous material 6 to 12.5 μ long and 4 to 8.5 μ wide, therewith often adhering to a passing nematode, thus capturing the animal, and then, after perforating its cuticle, giving rise internally, sometimes alone and sometimes in association with 1 to 15 convergent accessory infective branches usually 10 to 50 μ long, to colorless, branched, clamp-bearing assimilative hyphae 2 to 3.5 μ wide, which permeate the fleshy body lengthwise, appropriating its substance, and in some instances eventually pushing branches out through the cuticle to elongate externally. Ascending hyphae studded with clamp connections, colorless, sparingly branched, 2 to 3.5 μ wide, bearing conidia on conical sterigmata usually 1.8 to 7 μ long, 1.2 to 2.5 μ wide at the base, and 0.6 to 0.8 μ wide at the tip. Conidia colorless, cylindrical or elongated ellipsoidal, straight or slightly curved, broadly rounded at the distal end, often rather similarly rounded at the basal end though sometimes slightly narrowed proximally, mostly 10 to 23 μ long and 3.6 to 5.6 μ wide, at first continuous and filled throughout with protoplasm, after abjunction producing a glandular cell on the tip of a germinative protuberant outgrowth, then frequently, following successive elongation of the outgrowth, giving rise to 1 or 2 additional glandular cells, thereby becoming largely or wholly emptied of protoplasm and concomitantly partitioned by 1 to 4 cross-walls; the glandular cells of germinative origin measuring usually 4.5 to 6.5 μ in length and 2 to 2.5 μ in width, soon becoming surrounded by a globose or elongated ellipsoidal mass of adhesive material commonly 4 to 7 μ long and 3.5 to 6.5 μ wide.

Capturing and consuming *Panagrolaimus subelongatus* and *Ditylenchus* sp., and besides often parasitizing them, it occurs in decaying leaves and stems of *Bromus secalinus* near Hermiston, Oregon.

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EXPLANATION OF FIGURES

FIG. 1. *Nematoctonus concurrens*, drawn to a uniform magnification with the aid of a camera lucida; ×1,000 throughout. *A*, Portion of clamp-bearing mycelium from surface of agar plate culture: *a–c*, anastomoses of hyphae; *d*, sterigma bearing a conidium with which it is still continuous; *e–k*, sterigmata from which the conidia have become detached. *B*, Portion of prostrate hypha as seen undisturbed in a dry preparation when viewed directly from above: *a*, *b*, globules of adhesive material showing irregular pitting of surface whereby the glandular cell and supporting stalk are concealed from view; *c*, denuded sterigma. *C*, Same portion of clamp-bearing prostrate hypha as seen in a dry preparation when viewed from side: *a*, *b*, globules of adhesive material whose pitted surface obscures the glandular cell within, each thereby offering a false appearance of having been formed terminally by the supporting stalk; *c*, denuded sterigma. *D*, Portion of clamp-bearing prostrate hypha (for lack of space drawn in two parts connecting at point *z*) as seen in a moist preparation under a cover glass: *a–f*, erect predacious organs, showing the erect spurs supporting aloft the hour-glass-shaped glandular cell surrounded by the globose mass of adhesive secretion; *g–i*, sterigmata, each bearing a conidium. *E*, *F*, Portions of clamp-bearing prostrate hypha, each with an erect sterigma terminating in a young growing conidium. *G–J*, Portions of clamp-bearing prostrate hypha (though no clamp is shown in *H*), each with an erect sterigma still continuous with the full grown or nearly full grown conidium surmounting it. *K*, *L*, Portions of clamp-bearing prostrate hypha, each with an erect sterigma on whose empty tip is borne a mature conidium. *M*, Portion of clamp-bearing prostrate hypha with the proximal portion of an ascending branch, which is likewise studded with clamp-connections and bears three conidia, *a–c*, all about fully grown though not yet delimited at the base. *N* (*a–z*), *O* (*a–j*), Detached mature conidia, showing usual variations in size and shape. *P*, Portions of prostrate hypha, beset with clamp-connections and denuded sterigmata, which has anastomosed with a detached conidium nearby. *Q*, Conidia showing various stages of germination: *a*, conidium with several small vacuoles and young germ tube; *b–d*, conidia, each with an empty segment at one end and bearing at the other end an erect spur that supports a glandular cell surrounded by a globule of adhesive material; *e–i*, conidia, each with two empty segments at one end and bearing near the other end an erect spur surmounted by a glandular cell which is surrounded by a globule of adhesive material; *j*,

conidium with envelope almost entirely emptied of protoplasm, and containing three partitions, its contents having been used in the production of an unusually long germ hypha whereon is supported an adhesive glandular cell; *k*, conidium with two empty segments at one end, and bearing at the other end a germ tube, which, after degeneration of the first adhesive glandular cell produced by it, continued growth to produce a second; *l*, conidium with three empty segments at one end, its remaining live segment being continuous with an erect germ tube whereon two glandular adhesive cells are supported; *m*, conidium with an empty segment at each end, its living median segment being continuous with a germ tube whereon two glandular adhesive cells have been formed, the older, proximal one having already degenerated; *n*, conidium with four empty segments, its remaining live segment being continuous with a germ tube that has formed three glandular adhesive cells successively, the older two, however, having now degenerated.

FIG. 2. *Nematoctonus concurrens*, drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A*, Portions of two main prostrate clamp-bearing hyphae, *a* and *b*, as seen from above, in a dry preparation not covered with a cover glass; *c*, short anastomosing connection joining the two main hyphae where they cross one another; *d*, longer anastomosing connection between the two main hyphae; *e–o*, globules of adhesive material with irregularly indented surface whereby is obscured the glandular cell within; *p*, denuded sterigma. *B*, Same two portions of mycelial hyphae *a* and *b* as seen in a moist preparation flattened down under a cover glass; the anastomosing connections *c* and *d* showing little change, but the predacious organs *e–o* here appearing in longitudinal profile; *p*, denuded sterigma. *C*, *D*, Portions of prostrate clamp-bearing hyphae as seen in a moist covered mount, each portion showing two predacious organs, *a* and *b*, in longitudinal profile. *E*, *F*, Portions of prostrate clamp-bearing hyphae as seen in a moist covered mount, each showing three predacious organs, *a–c*, in longitudinal profile. *G*, Portion of clamp-bearing prostrate hypha as seen in a moist covered mount; *a–f*, six predacious organs shown in longitudinal profile. *H*, Portion of clamp-bearing prostrate hypha as seen in a moist covered mount; showing in longitudinal profile two predacious organs, one, *a*, bearing a single adhesive cell, the other, *b*, bearing three adhesive cells. *I*, Portion of clamp-bearing prostrate hypha as seen in a moist covered mount; showing in longitudinal profile four predacious organs, of which three, *a–c*, have each a single glandular cell, while the other, *d*, bears two degenerate adhesive cells in addition to the one adhesive cell in a functional condition. *J*, Portion of clamp-bearing prostrate hypha with a predacious organ, *a*, that has intruded two growing assimilative hyphae into a captured specimen of *Panagrolaimus subelongatus*. *K*, Portion of clamp-bearing prostrate mycelium showing one predacious organ, *a*, in an inactive state, and another such organ, *b*, which after capture of a specimen of *P. subelongatus* has intruded an assimilative hypha into the animal; *c–e*, three convergent supplementary infective branches, each of which has intruded an assimilative prolongation into the captive. *L*, Portion of clamp-bearing prostrate hypha showing in longitudinal profile three inactive predacious organs, *a–c*, and a fourth predacious organ, *d*, which after capture of a specimen of *P. subelongatus* has intruded an assimilative hypha into the

animal; *e–g*, three convergent supplementary infective branches whereof two have each extended an assimilative prolongation into the captive; *h–j*, denuded sterigmata. *M*, Portion of prostrate hypha with a clamp-connection that has given off a short branch terminating in an erect predacious organ, *a*.

FIG. 3. *Nematoctonus concurrens*, drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A*, Portion of clamp-bearing prostrate mycelium as seen in a moist covered mount; *a*, anastomosis of two hyphae; *b*, predacious organ in longitudinal profile. *B*, *C*, Portions of clamp-bearing prostrate hyphae as seen in a moist covered mount, each showing two predacious organs, *a* and *b*, in longitudinal profile. *D*, Portion of clamp-bearing mycelium, showing two predacious organs, *a* and *b*, in longitudinal profile. *E*, *F*, Portions of clamp-bearing prostrate hyphae, each with a lateral branch terminating in an erect predacious organ, *a*. *G*, Long clamp-bearing hyphal branch as seen in a moist covered preparation; showing two predacious organs in longitudinal profile, one, *a*, being attached laterally, the other, *b*, being borne terminally. *H*, Portion of clamp-bearing prostrate hypha bearing a partly degenerated predacious organ, *a*, and two other predacious organs, *b* and *c*, that have been operative in capturing a small specimen of *Ditylenchus* sp.; from *c* a short assimilative hypha has begun invasion of the animal. *I*, Portion of prostrate clamp-bearing mycelium, showing two hyphae joined together by a short anastomosing connection, *a*; two predacious organs, *b* and *c*, after being operative in capturing a specimen of *Panagrolaimus subelongatus*, have each extended an assimilative hypha into the animal; two convergent supplementary infective branches, *d* and *e*, have begun growing toward the captive. *J*, Portion of clamp-bearing prostrate mycelium comprising a nearly simple hypha, *a*, and a ramified hyphal system, *b*, whereof two main branches are united by an anastomosing connection, *c*; of the five inactive predacious organs, *d–h*, shown arising from the mycelium in longitudinal profile, three (*d–f*) have a single glandular cell, one (*g*) has two adhesive cells, and the fifth (*h*) has three adhesive cells, the lowermost one having in part degenerated; the predacious organ *i*, having been operative in the capture of a specimen of *P. subelongatus*, has sent an assimilative hypha into the animal; of the three convergent supplementary infective branches present, *j–l*, one likewise has intruded an assimilative hypha. *K*, Portion of clamp-bearing prostrate mycelium comprising three hyphae, *a–c*, joined together by the anastomosing connections *d* and *e*; *f–h*, inactive predacious organs, each having a single glandular cell; *i*, predacious organ that has been operative in capturing a specimen of *P. subelongatus*, and has intruded a branching assimilative hypha into the animal; *j–m*, convergent supplementary infective branches that have reached the animal and, with the exception of *k*, have each intruded an assimilative prolongation into it; numerous denuded sterigmata are shown on hypha *b*, and a few on hypha *c*. *L*, Posterior portion of a dead captured specimen of *P. subelongatus*, showing presence of clamps on assimilative hyphae, and external prolongation of two branches *a* and *b* that have broken out through the animal's integument. *M*, Portion of clamp-bearing ascending hypha with two sterigmata bearing the conidia *a* and *b*. *N–P*, Detached mature conidia, *a–z*, showing usual variations in size and shape.

FIG. 4. *Nematoctonus concurrens*, drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A*, Two clamp-bearing prostrate hyphae joined together by three short anastomosing connections, *a–c*; *d*, a predacious organ as seen in a dry uncovered mount. *B*, Portion of prostrate mycelium including three clamp-bearing hyphae, *a–c*, two of which are joined together by a short anastomosing connection, *d*; besides four predacious organs in an inactive state, *e–h*, there are present three predacious organs, *i–k*, that have operated in the capture of a specimen of *Ditylenchus* sp.; the two active organs *i* and *j* having invited development of the two convergent supplementary infective branches *l* and *m*, respectively. *C*, Portion of clamp-bearing prostrate hypha with one inactive predacious organ, *a*, and with another predacious organ, *b*, which after effecting the capture of a specimen of *Panagrolaimus subelongatus* has extended a branched assimilative hypha into the animal; a supplementary infective branch, *c*, besides has extended an assimilative prolongation into the captive. *D*, Portion of prostrate clamp-bearing hypha with a predacious organ, *a*, that after having effected capture of a specimen of *P. subelongatus* has sent a short assimilative hypha into the animal; two convergent supplementary infective branches, *b* and *c*, have begun growing toward the captured eelworm. *E*, Same hypha and captured nematode twenty minutes later; showing continued growth of the intruded assimilative hypha, and also further growth of the two convergent branches toward the place where the animal is affixed to the fungus. *F*, Same hypha and captured nematode one hour later than in *E*; showing further growth of the assimilative hypha extended from the predacious organ, and the intrusion nearby of an assimilative hypha from the convergent branch *b*; the convergent branch *c* has elongated only a little. *G*, Same hypha and captured nematode one hour later than in *F*; showing additional growth of the assimilative hypha first intruded and both growth and branching of the assimilative hypha coming from convergent branch *b*; as the convergent branch *c* has not elongated further, it has not yet penetrated into the animal. *H*, Portion of clamp-bearing prostrate mycelium with a predacious organ, *a*, which after being operative in capture of a specimen of *P. subelongatus* has extended an assimilative hypha into the animal; another assimilative hypha was at the same time intruded nearby from a predacious organ borne on a conidium, *b*, which consequently is empty of protoplasm; a supplementary infective branch, *c*, meanwhile grew to the place where the predacious organ from the conidium had penetrated into the captive. *I*, Posterior portion of dead captured specimen of *P. subelongatus*, showing branching and anastomoses of assimilative hyphae. *J*, Posterior portion of a dead captured specimen of *P. subelongatus* showing branching of assimilative hyphae, and prolongation externally of a filament that broke out through the integument at the tip of the animal's tail. *K*, Portion of prostrate clamp-bearing hypha with a sterigma bearing a mature conidium. *L*, *M*, Portions of strongly ascending aerial hyphae, showing origin of conidia at close intervals and close arrangement of clamp-connections. *N–P*, Portions of ascending clamp-bearing hyphae showing denuded sterigmata and rather closely spaced clamp-connections. *Q*, Random assortment of detached conidia, *a–z*, showing usual variations in size and shape.

OBSERVATIONS ON STREPTOMYCES GRISEUS. IV. INDUCED MUTATION AND STRAIN SELECTION *

EUGENE L. DULANEY, MYRLE RUGER AND CHARLES HLAVAC

(WITH 2 FIGURES)

One of the approaches to increasing the broth potency of a substance produced by a fermentation involves the putting into production of high yielding strains of the organism used in the fermentation. Such strains may be isolated from nature or may be natural or induced variants selected from strains already in use. The success possible with this approach is well exemplified by the published results of recent research on the development of *Penicillium notatum* and *P. chrysogenum* strains with an increased capacity for penicillin production (**1**, **7**).

The use of strain selection and induced mutation would seem to offer possibilities for increasing yields of streptomycin. The variability of actinomycetes is well known and streptomycin producing cultures are no exceptions. Schatz and Waksman (**8**) have already called our attention to the variability of *Streptomyces griseus*. Carvajal (**2**), in addition, has isolated numerous strains of this organism from nature. The above authors mentioned streptomycin production as one of the characters in which variation was noted. Moreover, Stanley (**9**) has successfully used strain selection to increase yields of streptomycin. By use of ultraviolet light treatment of spores and single colony isolation, he was able to obtain strains which produced striking yields when compared to the parent culture.

The present paper is concerned with some aspects of natural and induced variability in *Streptomyces griseus*, particularly in relation to streptomycin production.

* Contribution from the research laboratories of Merck & Co., Inc., Rahway, New Jersey.

METHODS

The original culture of *Streptomyces griseus* used in this work was received from Waksman's laboratory. Stock cultures were prepared by adding spores to sterile soil. As cultures were needed, spores were transferred from these soil stocks to Blake bottle slants of yeast extract-glucose agar. After good sporulation was obtained, sterile distilled water was added to the bottle and loose spores were washed free. This spore suspension was decanted into a sterile flask, shaken vigorously for several minutes and then filtered through several layers of sterile absorbent cotton. The effect of ultraviolet light was determined by exposing a portion of this spore suspension to ultraviolet light at a wave length of 2,537 Å for varying intervals of time. As a rule the time interval employed was sufficient to allow killing of more than 99 per cent of the spores. Treatment with $(ClCH_2CH_2)_3N$ was achieved by mixing another portion of the spore suspension in phosphate buffer at pH 8.0 with the $(ClCH_2CH_2)_3N$ at a final concentration of 0.005 M. After the desired treatment, the spores were diluted in a solution of 1 per cent glycine in distilled water. Natural variation was investigated by plating out diluted suspensions of untreated spores. In all of the above instances, surviving spores were plated out on yeast extract-glucose agar. The colonies that developed were transferred to slants of the same medium and allowed to sporulate. Spores from these cultures were used to inoculate the fermentation medium. This medium consisted of soy bean meal 20.0 gr., dextrose 10.0 gr., sodium chloride 10.0 gr., and distilled water 1 liter. The pH was adjusted to between 7.0 and 7.2 with 1 N sodium hydroxide before sterilization. The medium was dispensed in 40 ml. amounts in 125 ml. Erlenmeyer flasks, plugged with non-absorbent cotton and autoclaved at 121° C. for 20 minutes. After cooling, the flasks were inoculated and placed on a rotary-type shaker moving at a rate of 220 rpm. so that each flask described a circle 1.5 inches in diameter. The flasks were incubated at 28° C.

The cylinder plate method, employing pure streptomycin hydrochloride as the standard, was used for assay throughout the investigations.

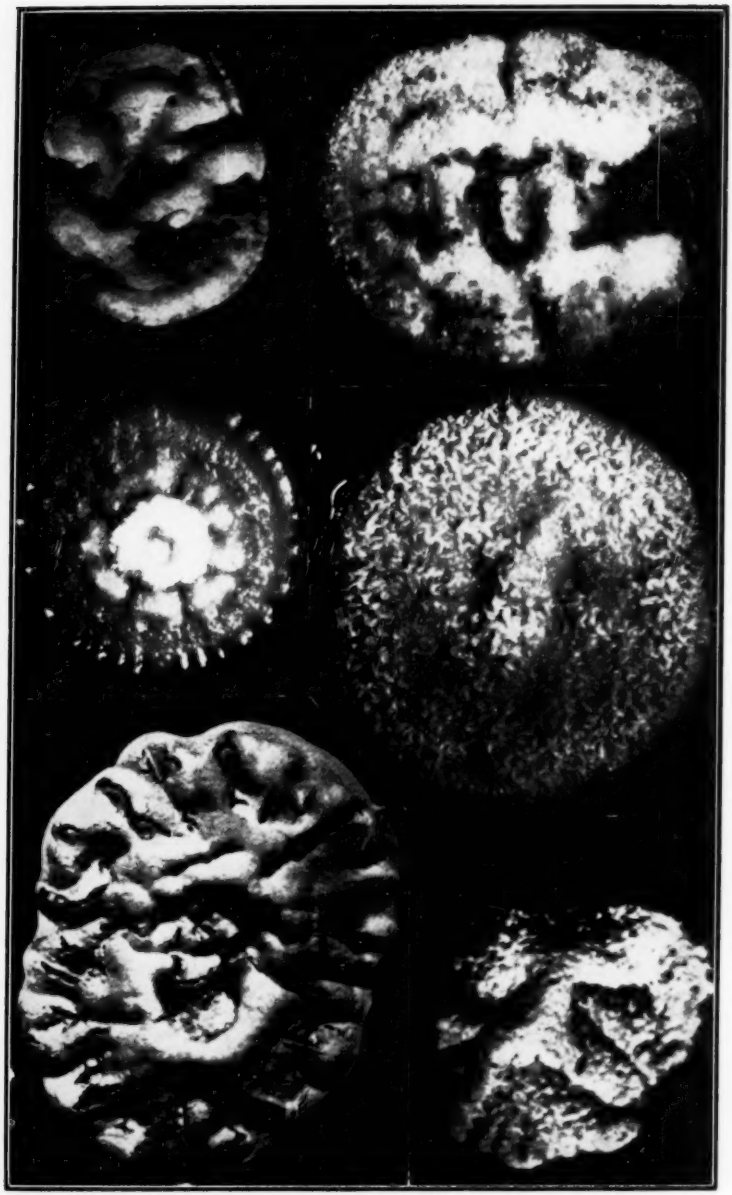

FIG. 1. Variants of *Streptomyces griseus;* all growing on yeast extract-glucose agar. × 4.

RESULTS AND DISCUSSION

Morphological variation. The amount of morphological variation depends upon the strain under observation. Some strains are morphologically quite stable, while others show a tremendous range of variation. Estimating the variation induced in these unstable strains as a result of treatment with ultraviolet light or $(ClCH_2CH_2)_3N$ is understandably difficult. It is quite obvious, however, that treatment of spores with both of these agents results in severe morphological change. Variants, that have not as yet been obtained from untreated spores, can be obtained after treatment. In addition, the incidence of the variants that are obtained without any treatment is increased by the above treatments. One of the most variable characters is the degree of sporulation. Cultures range from the parental type to types which form no spores at all. Not only the amount of sporulation but spore color is variable. The color range is from gray-green through light buff to pure white. This variation in amount of sporulation and in color of spores results in a marked variation in the colony appearance. Further changes can be seen in the margin and surface of the colony as well as in colony sectoring. The amount of exudate on the colony surface, as well as the amount and color of the soluble pigment released into the medium, varies among mutants. Changes in the amount and color of the pigment produced are often striking. The usual range in pigmentation is from none through a light yellow to a deep brown to black. Frequently, however, mutants are obtained which produce a diffusible pale pink to deep pink pigment. These observations were made with cultures growing on yeast extract-glucose agar. Media probably could be devised which would show these pigment changes to greater advantage.

Examples of ultraviolet light induced mutants are shown in figure 1.[1]

Attempts have been made to correlate productive capacity with morphological type. Detailed observations of a large number of mutants have shown some correlation but in no case is this correlation complete. One strain studied in detail was a near-albino

[1] Acknowledgment is made to Mr. Jack Kath of the Merck Institute for Therapeutic Research for preparation of these photographs.

sporulating mutant which was quite stable morphologically. Study of more than 1,000 isolates from this culture resulted in one striking correlation between production and morphology. A number of cultures showed a ragged appearance with reduced sporulation and development of phage-like plaques. These cultures were significantly better than the parent, the correlation between production and morphological appearance being almost perfect.

Another strain studied in detail was a gray-green sporulating type. This was the most unstable culture that has thus far been examined. Two general types were isolated from it. One was the normal gray-green sporulating type which exhibited little variability in morphology or capacity for producing streptomycin. The other type could be conveniently termed albino, though it was certainly a heterogeneous mixture of albino types. Production by isolates of this latter group ranged from nothing to very high values. There was within this albino group no correlation between morphological type and streptomycin production. While it may be noted that all promising cultures isolated from this strain were of the albino type, it was likewise true that all isolates incapable of producing streptomycin were of the same type.

Results, then, would indicate that detailed investigation of one strain may reveal some correlation between productive capacity and morphological type. Such a correlation, however, will probably not hold true for a different strain. Thus far, no definite correlation between morphological character and productive capacity has been found. Although such a correlation may seem to exist if a relatively small number of isolates are investigated, it disappears if a detailed examination of large numbers of cultures is made.

Schatz and Waksman (**8**) have reported the isolation of cultures which produced no aerial mycelium and no streptomycin. From these cultures sporulating isolates were obtained which again produced streptomycin. Such cultures have been isolated in this and, undoubtedly, in other laboratories. Not all of these non-sporulating cultures, however, lack the ability to produce streptomycin. Some are capable of producing relatively high yields. In table I is shown the productivity of seven non-sporulating single colony isolates selected at random from a sporulating streptomycin producing strain.

Structurally these non-sporulating strains are probably composed of the substratum mycelium of Ørskov (**6**) or the primary mycelium of Klieneberger-Nobel (**5**). The lack of aerial or secondary mycelium may be due to the failure of the "initial cells," discussed by Klieneberger-Nobel (**5**), to organize.

Non-streptomycin producing strains. Sporulating strains, as well as non-sporulating strains, can be isolated which lack the ability to produce streptomycin. The incidence of these zero strains can be increased by treatment with ultraviolet light.

It was thought possible that the failure of these strains to produce streptomycin was due to their inability to synthesize various portions of the streptomycin molecule. If this were true it might be possible to obtain streptomycin production from these cultures by inoculating fermentation medium with spore mixtures of zero mutants which produced complementary portions of the streptomycin molecule. In addition, if the unsynthesized portion(s) of the streptomycin molecule was (were) supplied, single cultures might again produce streptomycin. These suppositions are predicated by the ability of the organism to unite the various portions of the molecule, when they are present, even though the portions under consideration might not be synthesized first and then united in the regular course of biosynthesis. However, when medium was inoculated with spore mixtures of these zero strains, no streptomycin was formed. In addition, when various parts of the streptomycin molecule were added singly and in combination to media inoculated with zero strains, negative results were again obtained.

It should be noted, however, that this work was done with only a few strains. The physiology of these strains would be similar if the formation of streptomycin were interrupted in each case by a mutation at the same gene position. In this event, similar intermediates would accumulate and the strains would react similarly to the addition of possible streptomycin precursors. In addition, if a fermentation medium is inoculated with a mixture of such cultures the negative results noted above are to be expected. Investigation of a group of cultures, in which the ability to synthesize streptomycin has been interrupted by mutations at different gene positions, may aid in isolating streptomycin intermediates and thus serve to determine the mechanism of biosynthesis.

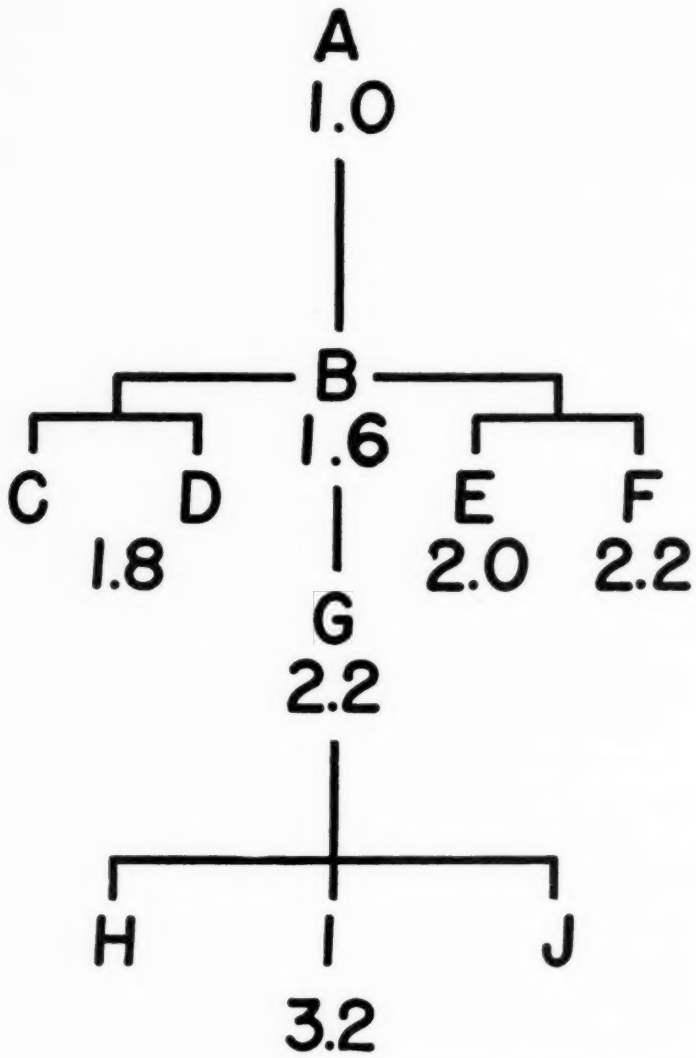

FIG. 2. Diagram illustrating increase in streptomycin production by successive isolation of mutants with increased capacity for production.

Strains with increased productive capacity. One of the reasons for undertaking a study of normal and induced variation in *Streptomyces griseus* was to determine if strains could be selected which possessed an increased capacity for streptomycin production. The results, in part, are summarized in figure 2. The broth potency produced by strain A is taken as unity and the productivity of selected strains is compared to strain A.

Spores from strain A were treated with ultraviolet light, and cultures which developed from the surviving spores were tested for streptomycin production. One of these cultures, B, produced 60 per cent more streptomycin than strain A, or 1.6 times as much. Spores from strain B were likewise treated with ultraviolet light. Two cultures thus obtained, C and D, produced approximately 12.5 per cent more streptomycin than the parent strain B, or 1.8 times as much as strain A. Although these yields are not striking, as compared with those obtained from the parent culture B, they represent a significant increase and are reproducible over a large number of retests. Spores of strain B were also treated with $(ClCH_2CH_2)_3N$. Two cultures, E and F, which produced 25 per cent and 37.5 per cent more streptomycin than strain B, were so obtained. These strains produce 2.0 and 2.2 times as much streptomycin as strain A. These cultures, however, rapidly lost the ability to produce streptomycin, thus making further work with them impractical. The most promising culture isolated from strain B was strain G. This strain was obtained as a single colony isolate by plating untreated spores of strain B on yeast extract-glucose agar. It is morphologically similar to its parent and consistently produces streptomycin yields 37.5 per cent higher than the yields produced by the parent strain B, or broth potencies 2.2 times as high as are produced by strain A. Spores of strain G were treated with ultraviolet light, the survivors allowed to develop on yeast extract-glucose agar, and the resulting colonies isolated and tested. From approximately 150 isolates thus tested, three cultures were obtained which produced approximately 45.5 per cent more streptomycin than strain G. These cultures, H, I, and J, produce 3.2 times as much streptomycin as the original strain A.

Further mutation and selection of the highest producing strains has been carried out. The above results, however, are sufficient

to show how induced mutation and strain selection can be used to increase streptomycin production. When one is undertaking such selection, however, it must be understood that the cultures are being tested for production under the set of conditions being used. Cultures thus found to produce high yields should not necessarily be expected to produce corresponding yields with changed conditions. Changes in the fermentation environment may have varying effects on different strains. Medium specific mutants should be expected.

It would be very enlightening if the physiological changes resulting in increased streptomycin productivity could be determined. With this in mind, some investigations of the physiology of various mutants have been made. Although some physiological differences between various mutants have been found, nothing indicates why one strain is capable of producing more streptomycin than the other.

The improved broth potencies noted above are not confined to experiments made on media composed partially of complex plant and animal material. Relatively high yields have been obtained on well defined simple synthetic media (**3**) (**4**).

TABLE I

STREPTOMYCIN PRODUCTION BY NON-SPORULATING STRAINS OF *Streptomyces griseus*

Culture Number	Maximum Yield γ/ml.	Day of Maximum
1	100	5
2	0	—
3	0	—
4	390	5
5	0	—
6	43	4
7	469	5

SUMMARY

1. The normal variation found in *Streptomyces griseus* can be increased by treatment with either ultraviolet light or $(ClCH_2-CH_2)_3N$.

2. Some of the variable characters include the color of spores and degree of sporulation; the surface and margin of the colony, as well as colony sectoring; the amount and color of exudate on the colony surface; and the amount and color of soluble pigment released into

the substratum. In addition, great variation occurs in the amount of streptomycin produced.

3. No complete correlation between morphological type and streptomycin production could be found.

4. Strain selection and induced mutation can be used to obtain strains with an increased capacity for producing streptomycin.

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THE EFFECT OF TEMPERATURE ON THE PAPILLATION OF OOGONIA OF ACHLYA COLORATA

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(WITH 6 FIGURES)

Achlya colorata can be clearly distinguished from its closest relative, *Achlya racemosa,* by the difference in the diameters of their oospores as well as by differences in such minor features as relative abundance of gemmae. However, the specific status of *A. colorata* was long debated because of the irregularity of the appearance of the papillate oogonia which were regarded by early investigators as the most important specific characteristic of this fungus.

A. colorata was first described by Cornu (**1872**) as *A. racemosa* var. *stelligera* and *A. racemosa* var. *spinosa.* Pringsheim (**1882**) renamed these varieties *A. colorata,* primarily on the basis of oogonial papillation. Fischer (**1892**), finding smooth and papillate oogonia on the same hyphae, considered *A. colorata* to be the same as *A. racemosa.* Minden (**1912**) continued to follow Cornu, describing in addition a form, *Pringsheimii,* of *A. racemosa* with "a few projections which may give the oogonia an angular appearance" and slightly fewer oospores. It remained for Coker (**1923**) to point out that "It is true that smooth or nearly smooth oogonia may appear rarely in this species, but they are not the oogonia of *A. racemosa,* which are always easily recognized by their much smaller eggs." The oospores of *A. racemosa* are mostly about 22 μ in diameter, those of *A. colorata* mostly 30–37 μ. Coker also states that "We have never seen a perfectly smooth oogonium in *A. colorata* or a papillate one in *A. racemosa.*" This has not been true of our cultures of *A. colorata.*

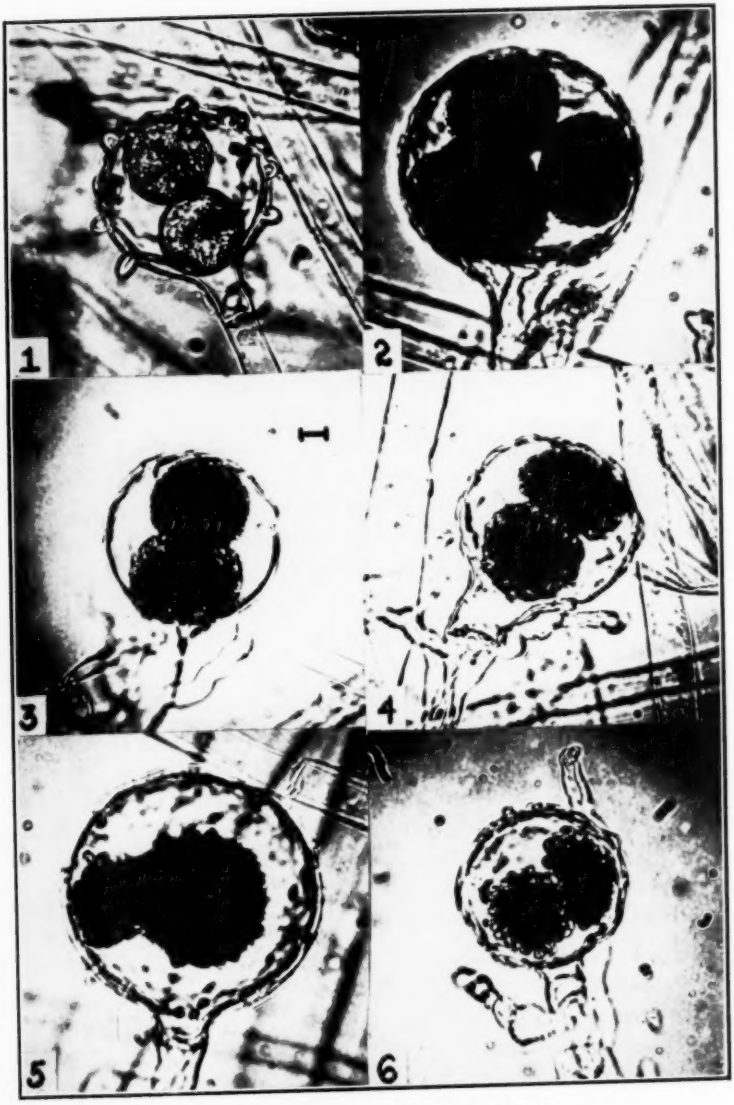
It is curious, since it has been known for so long that temperature affects not only quantitative, but also qualitative characteristics

of living organisms, that mycologists working with the Saprolegniaceae, and with many other groups of fungi, have in the past paid so little attention to the temperatures at which the cultures they have described were grown. The effect of temperature on papillation in this fungus came to my attention more or less accidentally: a mycelial mat (derived from a single-spore culture which had been previously identified as *A. colorata* when grown on hemp seed at 15° C.) grown in pure culture at 25° C. produced apparently smooth oogonia. This culture was then incubated at 15° C. for two days, during which period papillate oogonia appeared.

In order to determine more precisely the effect of temperature on papillation in *A. colorata*, cultures were grown, on several media, at temperatures ranging from 10 to 30° C. at 5° intervals. No growth occurred at 30° C. on any of the media used. Three single-spore isolates of *A. colorata*, from a collection of soil, made in Palisades Interstate Park, N. J., were used in these experiments: in the later experiments a culture derived from a single hyphal tip from an isolate obtained from Dr. Shanor was also employed as inoculum.

Unifungal cultures on boiled halves of popcorn and hemp seed in petri dishes containing charcoal-treated distilled water gave somewhat equivocal results. On both of these substrates oogonia were invariably papillate at 10 and 15° C., though papillation was rather more regular at the higher temperature. The first oogonial initials appeared in five to six days at 10° C., three days at 15° C. Oogonia appeared in two days in cultures incubated at 20° C., but when the cultures were examined on the fifth day a minority of the oogonia were atypical, with fewer, shorter papillae than at 15° C., or rarely with the surface of the oogonium merely uneven. This tendency toward the suppression of papillae was marked in cultures grown at 25° C., though even here only approximately half of the oogonia, mainly those nearer the substrate, showed atypical characteristics ranging from possession of only one or two papillae to complete smoothness of the oogonial surface.

In order to minimize the effects of uncontrolled variable factors—such as food and oxygen and bacterial contamination (which sooner or later always became evident in the unifungal cultures)—*A. colorata* was then grown in pure culture on both liquid and solid media. Difco corn meal agar to which 0.5 g./l. of yeast extract had



FIGS. 1–6. Oogonia of *Achlya colorata*.

been added was used as the solid medium. Cultures grown on this agar in petri dishes gave the following results: At 10 and 15° C. papillate oogonia appeared in eight and four days respectively. At 20° C. the oogonia, appearing from the second day of growth, were usually roughened or with a few short papillae, infrequently reaching the extremes of normal papillation (as described for the species) or of complete smoothness of surface. At 25° C. the oogonia formed were roughened or completely smooth, never papillate, aborting or producing oospores which were nearly all aborted by the eighth day of growth. The position of the oogonia in the agar or on the surface of the agar did not obviously affect papillation.

The liquid medium employed consisted of 5 g./l. of yellow corn meal (as an extract made by boiling with distilled water ½ hour and centrifuged clear before use), 1 g./l. of yeast extract and 5 or 2.5 g. l. of glucose. There was no difference in papillation associated with the difference in concentration of glucose. *A. colorata* was grown in 20 ml. portions of this broth in 250 ml. Erlenmeyer flasks until the appearance of the first oogonial initials (at 7–10, 5, 3 and 3 days for cultures incubated at 10, 15, 20 and 25° C. respectively), when the mats were transferred, without washing, to sterile charcoal-treated distilled water in petri dishes. The mats matured more normally, though papillation was not markedly affected, when treated in this way than when allowed to remain in the culture broth. It was found that sexual reproduction was inhibited by washing the mycelia. Results were as follows: Oogonia were never formed in abundance at 10° C. and those formed were somewhat atypical and aborted. At 15° C. papillate oogonia were produced. An oogonium typical both of the cultures grown at 15° C. and of the species as described is shown in figure 1. The papillae, 6–10 μ long, are set regularly about the entire surface of the oogonium. The number of papillae may be slightly fewer than in this figure or sometimes greater, with occasional papillae touching at their bases or fused along their sides. The oogonia, irregularly set with short papillae, or merely roughened, shown in figures 2, 3 and 4, are typical of about 90 per cent of those appearing at 20° C. Oogonia typical of about the same percentage of those produced at 25° C. are shown in figures 5 and 6 as roughened or with 1 or

2 short papillae. None was as papillate as any of the oogonia produced in the 15° C. cultures. A completely smooth oogonium was rarely seen. The oospores almost invariably aborted.

It seems likely that the differences of opinion regarding papillation of the oogonia of *A. colorata* have been caused by differences in temperature in the laboratories in which this fungus has been studied. Pure cultures, grown under described conditions, should be used for the description of species. The use of mixed or even of unifungal cultures may have contributed to the confused status of many species of the Saprolegniaceae and should be discouraged.

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EXPLANATION OF FIGURES

FIGS. 1–6. Oogonia of *Achlya colorata* from pure cultures grown in broth. × 400. The photomicrographs were taken with a Leica Makam, using a 10 × ocular and a 44 × objective. The line drawn on figure 3 indicates the relative length of 10 μ. FIG. 1. An oogonium from a mat incubated at 15° C. FIGS. 2, 3 and 4. Oogonia from mats incubated at 20° C. FIGS. 5 and 6. Oogonia from a mat incubated at 25° C. The oospores in both oogonia are already beginning to degenerate.

AMINO ACIDS IN THE BIOSYNTHESIS OF PENICILLIN

FREDERICK T. WOLF

Several investigations have been concerned with amino acids as sources of nitrogen for the production of penicillin. Foster *et al.* (**1943**) were apparently the first to test individual amino acids as sole sources of nitrogen for penicillin production by *Penicillium notatum* in surface cultures, finding that nitrate nitrogen was superior to amino acids. In subsequent experiments with submerged cultures, these workers (**1946**) noted that glutamic acid was superior to asparagine or glycine as a nitrogen source for one mold strain tested. With another strain, however, various single amino acids did not promote penicillin formation in the basal medium, either with or without additional sources of nitrogen.

Large increases in penicillin yield obtained in media containing corn steep liquor were found by White *et al.* (**1945**) to be at least partially due to arginine, histidine and glutamic acid. When a mixture of these compounds, in concentrations of 30 mg., 30 mg., and 400 mg. per 100 ml., respectively, was added to a basal medium containing glucose, lactose and mineral salts, yields assaying 80–90 per cent of that obtained in corn steep media resulted. This finding suggested that amino acids might be involved in the biosynthesis of penicillin: "It would appear that in some way this mold is perhaps able to convert one or several of the amino acids to a part of the penicillin molecule through its metabolic processes." It was further shown that hydrolyzed corn steep liquor is unsatisfactory for penicillin production, in comparison with hydrolyzed protein-free liquor, the large increase in free amino acids resulting in conditions unfavorable for penicillin formation.

Halpern *et al.* (**1945**) reported increased penicillin production upon the addition of proline or glutamic acid to synthetic media. Aspartic acid could be substituted for glutamic acid, and the addition of arginine also had a slight stimulatory effect. A number of

other amino acids, however, including histidine, methionine, tryptophane, hydroxyproline and phenylalanine, were ineffective.

Stone and Farrell (**1946**) failed to obtain consistent increases in penicillin yield upon the addition of most of the common amino acids to synthetic media, although occasional increases sometimes followed the addition of leucine, cystine or cysteine. Cook and Brown (**1946**) recorded increased yields upon the simultaneous addition of glucose and leucine or glucose and tyrosine, although the addition of the amino acids alone gave only a slight stimulatory effect.

In a subsequent paper (**1947**) these same workers studied more thoroughly the influence upon penicillin yield in surface cultures of the addition of various amino acids to a basal medium containing $NaNO_3$. The amino acids were added in such quantities as to provide a nitrogen content (exclusive of $NaNO_3$) of 140 mg. per cent. Under these conditions, small increases in penicillin yield were obtained with *dl*-tyrosine, serine, cystine, *dl*-aspartic acid, glutamic acid, arginine, histidine, *dl*-tryptophane, proline and asparagine. Glycine, alanine, valine, *d*-isoleucine, phenylalanine, *l*-dihydroxyphenylalanine, methionine or *dl*-lysine, however, had no stimulatory action on penicillin formation. No correlation between stimulatory effect upon penicillin yield and chemical structure of these compounds was possible.

Bonner (**1947**) tested alanine, serine, valine, cystine and methionine as possible penicillin precursors in surface and submerged cultures. Experiments using combinations of mutant "penicillinless" strains, to which these compounds were supplied singly, in the presence of phenylacetic acid, and in the presence of *dl*-penicillamine, yielded completely negative results.

Cardinal and Hedrick (**1948**) have recently presented analyses of the amino acid content of corn steep liquor. A corn steep liquor hydrolysate was found by microbiological assay to contain alanine in excess of 27 per cent of the nitrogen present, large amounts of arginine, glutamic acid, histidine, leucine, proline, lysine, valine, threonine and isoleucine, as well as smaller quantities of phenylalanine, aspartic acid, cystine, methionine and tyrosine.

The present study was undertaken because of the diversity of results obtained concerning the role of various amino acids in the

biosynthesis of penicillin, resulting in part from the use of different mold strains and a variety of basal media by various workers. Further, no data of this type are available concerning *Penicillium chrysogenum* Q-176, the strain employed in almost all commercial penicillin production at the present time.

MATERIALS AND METHODS

P. chrysogenum Q-176 was employed in the present experiments. Stock cultures were maintained on slants of Czapek's agar. The basal medium for submerged cultures was adapted from one developed by Moyer and Coghill (**1946**) and has the following composition: lactose monohydrate, 27.5 g.; glucose monohydrate, 3.0 g.; $MgSO_4 \cdot 7H_2O$, 0.25 g.; KH_2PO_4, 0.50 g.; $ZnSO_4 \cdot 7H_2O$, 0.044 g.; and $MnSO_4 \cdot 4H_2O$, 0.020 g. per liter. To this basal medium were added various amino acids as sole sources of nitrogen, in quantities sufficient to provide a nitrogen concentration of 50 mg. per cent. Controls were provided in which the nitrogen was supplied as $NaNO_3$ (50 mg. per cent of nitrogen) or as corn steep solids (22.0 g. per liter). No phenylacetic acid or other penicillin precursor was added to the media; hence the penicillin produced, except in the series containing corn steep solids, was probably largely penicillin K (Higuchi *et al.*, **1946**).

The cultures were grown at room temperature, in Erlenmeyer flasks of 500 ml. capacity containing 100 ml. of medium. The cultures were continuously agitated by means of a reciprocating shaker operating at the rate of 100 strokes per minute, with a stroke length of 7.0 cm.

All penicillin assays were performed on filtrates of cultures 7 days of age. The assay for total penicillins was carried out by means of the dilution technique, using *Staphylococcus aureus* H as the test organism. The broth from the *Penicillium* cultures was removed under sterile conditions, dilutions of 1 : 5, 1 : 25, 1 : 125, 1 : 625 and 1 : 3125 were made in tubes of Difco Heart Infusion Broth, and each tube was inoculated with 0.1 ml. of a 24 hr. culture of *S. aureus*. The tubes were incubated at 37° C. and read after 18 hrs. After determination of the highest dilution inhibiting growth and the lowest dilution with apparent turbidity, an aliquot of the penicillin broth, which had been stored in a refrigerator, was reassayed.

For the reassay, another series of five tubes was prepared, including the concentrations of penicillin immediately above and below the end point of the preliminary assay, with three intermediate concentrations interpolated. The highest dilutions inhibitory to growth of *S. aureus* are included in table I.

The sensitivity of *S. aureus* H, using commercial penicillin G as a standard, was determined to be 0.030 units/ml. This value was checked repeatedly during the course of the experiments, and, as no variation was found, it was employed in the conversion of dilution units to Oxford units.

RESULTS

Good growth of *P. chrysogenum* was obtained with each of the 24 amino acids tested, with the exception of cystine and cysteine.

TABLE I

PENICILLIN PRODUCTION BY *P. chrysogenum* Q-176 FROM VARIOUS AMINO ACIDS

Amino Acid	mg./100 ml.	Max. Dilution Inhibitory to *S. aureus*	Penicillin Yield, Oxford units/ml.
Glycine	269	1:625, 1:625	19
dl-Alanine	318	1:375, 1:1250	24
beta-Alanine	318	1:1250, 1:3125, 1:625, 1:625	42
dl-Serine	376	1:125, 1:1250	20
dl-Threonine	427	1:250, 1:625	13
l-Arginine·HCl	188	1:125, 1:125	4
l-Aspartic acid	476	1:375, 1:375, 1:625	14
l-Asparagine	236	1:500, 1:625, 1:625	18
l-Glutamic acid	526	1:1250, 1:250, 1:625	21
l-Proline	410	1:625, 1:250, 1:250	11
l-Hydroxyproline	467	1:1250, 1:1250, 1:250	27
l-Leucine	467	1:25, 0, 1:25	0.50
dl-Isoleucine	467	1:5, 1:5, 1:5	0.15
dl-Norleucine	467	0, 0, 0	0
dl-Valine	420	1:5, 1:5, 0	0.10
l-Histidine·HCl	228	0, 1:5, 0	0.05
l-Lysine·HCl	327	0, 0, 0	0
l-Cystine[1]	431	0, 0, 0[2]	0
dl-Methionine	532	0, 0, 0	0
l-Cysteine·HCl	562	—, —, —[3]	0
l-Tryptophane	365	0, 0, 0	0
l-Tyrosine[1]	649	1:25, 1:25, 1:25	0.75
dl-Phenylalanine	588	0, 0, 0	0
$NaNO_3$	300	1:3125, 1:2500, 1:625, 1:2500	66
Corn steep solids	2200	1:6250, 1:6250	187

[1] Insoluble. [2] Only a trace of growth. [3] No growth, no assay made.

Only a trace of growth was obtained in media containing cystine. Microscopic examination showed that spore germination occurred, but mycelial growth was very restricted. This observation is in agreement with the finding (Wolf, **1948**) that cystine is not oxidized by this strain of *P. chrysogenum*. Cysteine monohydrochloride was evidently toxic in the concentration employed, as germination was completely inhibited.

Although no quantitative determinations of the amount of mycelial growth were made, it was apparent that proline and glutamic acid are particularly favorable for growth of *P. chrysogenum*. Alanine, which was previously shown (Wolf, **1948**) to be respired at a very rapid rate by this strain, did not support as luxuriant mycelial growth as did proline or glutamic acid.

In table I are included the various amino acids tested, the quantity of each which was used (equivalent to 50 mg. per cent of nitrogen) and the results of penicillin assays from 2–4 experiments with each amino acid.

DISCUSSION

In explanation of the apparently low yields obtained in cultures with $NaNO_3$ or corn steep solids as the nitrogen source, it should be borne in mind that the higher yields of commercial penicillin production employing this strain are obtained with media containing both $NaNO_3$ and corn steep solids, and supplemented by phenylacetic acid or other penicillin precursors. From the data presented it is evident that *P. chrysogenum* is able to achieve a total synthesis of penicillin from the basal medium when supplemented with certain amino acids as sole sources of nitrogen. These include several amino acids of low molecular weight, including glycine, alanine, beta-alanine, serine and threonine; the dicarboxylic compounds, glutamic acid and aspartic acid; asparagine; proline and hydroxyproline; and arginine.

The low values obtained with leucine, isoleucine, valine, histidine and tyrosine are believed not to be significant, in view of the possibility of the presence of small quantities of impurities in the amino acids used. Essentially negative results were thus obtained with cystine, cysteine, methionine, histidine, lysine, leucine, isoleucine, norleucine, valine, tryptophane, tyrosine and phenylalanine. The

results with cystine and cysteine are necessarily inconclusive, since mycelial growth is a prerequisite for penicillin formation.

No explanation is readily apparent for the finding that certain amino acids are able to participate in the biosynthesis of penicillin, while others cannot. The suitability of a given amino acid for penicillin formation cannot be correlated with its rate of oxidation by *P. chrysogenum* (Wolf, **1948**), or with its suitability for mycelial growth. The fact that only amino acids with six or fewer carbon atoms are effective, and that a number of these are closely related structurally or metabolically, would suggest that the carbon skeleton may be important. It has recently been shown by Knight (**1948**) that *P. chrysogenum* Q-176 deaminates both alanine and methionine, liberating one molecule of ammonia for each atom of oxygen consumed. Therefore, penicillin formation from methionine is not blocked by failure of deamination to occur. This would suggest that the various keto-acids resulting from amino acid deamination might be most important in relation to penicillin biosynthesis.

Moderately good agreement was obtained with the findings of Cook and Brown (**1947**). Identical results were obtained in each case with serine, aspartic acid, glutamic acid, arginine, proline and asparagine, which take part in penicillin formation, and with valine, isoleucine, phenylalanine, methionine and lysine, which do not. The results do not agree in the case of tyrosine, cystine, histidine, tryptophane, glycine and alanine. Further, the present results are in agreement with those of Halpern *et al.* (**1945**), except in the case of hydroxyproline. The discrepancies noted are probably attributable to the use of different mold strains, which may well exhibit metabolic differences of this character.

None of the amino acids proved superior to nitrate as a nitrogen source for penicillin formation, thus confirming the finding of Foster *et al.* (**1943**) with surface strain of *P. notatum*.

In addition to other known functions of corn steep liquor in promoting penicillin formation, it would appear from the present data that the suitability of this material is due, at least in part, to its content of the amino acids usable in penicillin biosynthesis; namely, alanine, arginine, glutamic acid, proline, threonine, and aspartic

acid, which together, according to Cardinal and Hedrick (**1948**), make up about 54 per cent of its nitrogen content.

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SUMMARY

When grown on a basal medium with the addition of single amino acids as sole sources of nitrogen in quantities equivalent to 50 mg. per cent of nitrogen, *Penicillium chrysogenum* Q-176 is able to produce small amounts of penicillin from glycine, alanine, beta-alanine, serine, threonine, arginine, aspartic acid, asparagine, glutamic acid, proline, and hydroxyproline. No penicillin is produced from leucine, isoleucine, norleucine, valine, histidine, lysine, cystine, methionine, cysteine, tryptophane, tyrosine, or phenylalanine under identical conditions. None of the amino acids tested is superior to nitrate as a source of nitrogen for penicillin biosynthesis.

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CHROMOSOME NUMBERS IN THE HYPOCREACEAE

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(WITH 2 FIGURES)

The use of smear techniques (McClintock, **1945**; Cutter, **1946**) recently has advanced the study of chromosomes in the ascomycetous fungi. The present paper reports a brief survey, carried out with such methods, of the chromosome numbers of several species belonging to different genera of the family Hypocreaceae.

It has recently been shown that homothallic forms of *Hypomyces solani* Rke. et Berth. emend. Snyd. et Hans. (FIGS. 1F and 2F) have six chromosomes in the haploid stage (Hirsch, **1949** [1]), while the heterothallic *H. solani* f. *cucurbitae* Snyd. et Hans. may have four (FIGS. 1E and 2E), three or two chromosomes, depending on the sex of the isolate (Hirsch, **1947**). It was therefore of interest to examine the chromosome number of the closely related genera *Gibberella, Calonectria* and *Nectria.* We have so far studied only species of these genera in which there is a conidial stage belonging to the imperfect genus *Fusarium.* The following were studied: *Gibberella roseum* Lk. emend. Snyd. et Hans. (homothallic), *G. lateritium* Nees emend. Snyd. et Hans. (heterothallic?), *Calonectria rigidiuscula* (Berk. et Brme.) Sacc. (homothallic), *Nectria episphaeria f. coccophila* (Desm.) Snyd. et Hans. (heterothallic?).

Perithecia were obtained in the first three fungi by growing them on water agar, to which was added ground up wheat straw sterilized by propylene oxide vapor (Hansen and Snyder, **1947**), outside a north window. In the case of *Nectria* a small piece of a twig infested with scale insects, but also subjected to gaseous sterilization, was substituted for the wheat straw (Snyder and Hansen, **1947**). The perithecia were fixed and smear preparations of the asci prepared and stained by the method referred to above.

[1] Hirsch, Hilde E. The cytogenetics of sex in *Hypomyces solani* f. *cucurbitae.* Amer. Jour. Bot. **36**: 113–121. 1949.

Both *Gibberella lateritium* and *G. roseum* (FIGS. 1A, 1B and 2A, 2B respectively) proved to have six pairs of chromosomes in the fusion nucleus. *Calonectria* (FIGS. 1C and 2C) and *Nectria* (FIGS. 1D and 2D), on the other hand, have seven.

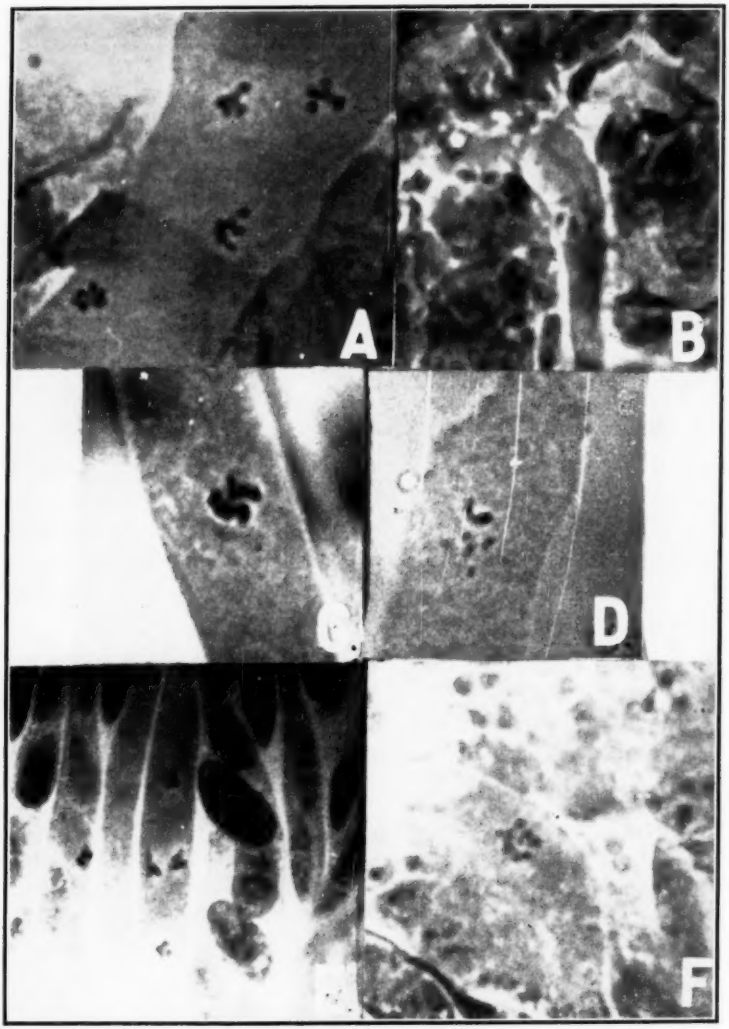

FIG. 1. Chromosome numbers in the Hypocreaceae.

No detailed study of the relative size and the morphology of the different chromosomes has been attempted so far. There is a remarkable uniformity in the cytology of all the species of Hypocreaceae studied by us, except for the *Nectria*. Here the asci are

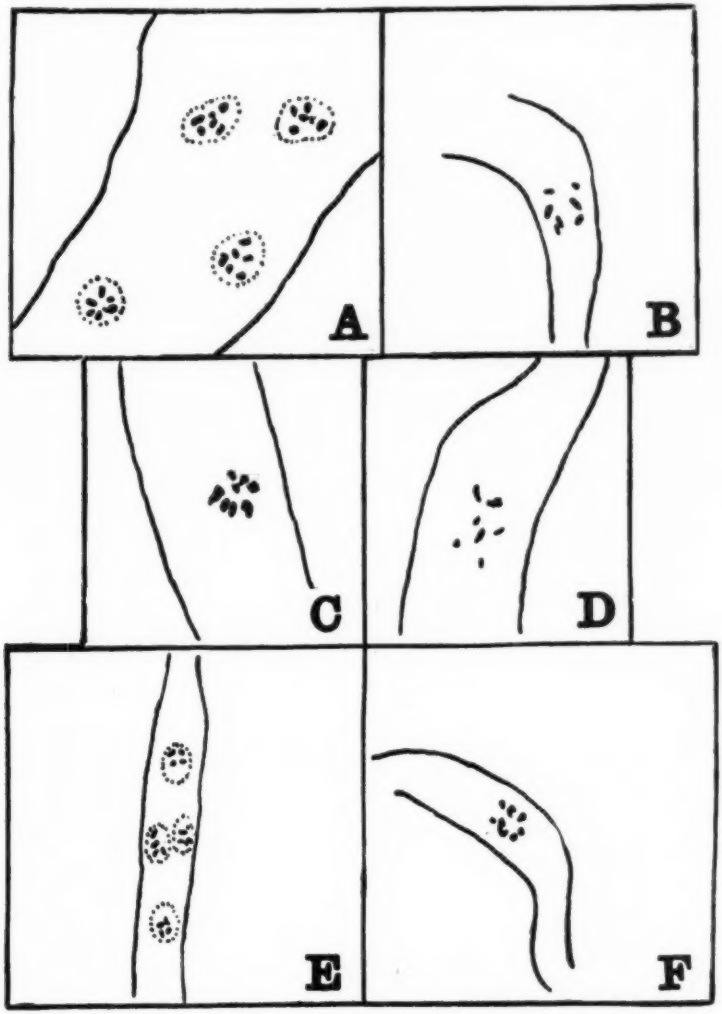

FIG. 2. Drawings interpreting fig. 1.

interspersed with sterile cells, and they react differently to stains. Although the other species were stained with Barrett's haematoxylin or acetocarmine, and could not be stained with the acetic orcein used, only the latter stain was effective on *Nectria*. There is also a remarkable difference in the size of the nucleolus (up to 4.5 μ in diameter during early meiotic prophase in *Nectria*, and up to 2.6 μ in *Hypomyces*).

It has been suggested (Snyder and Hansen, **1945**) that the generic distinction between *Nectria* and *Hypomyces* is doubtful in those species which have *Fusarium* imperfects. Similarly, the validity of retaining both the genera *Gibberella* and *Calonectria* has been questioned. Although the difference in chromosome number would appear to suggest a possible basis for distinction between genera in these two cases, it must be remembered that different chromosome numbers frequently occur within a single species, as has been shown in *H. solani* (Hirsch, **1947**). Much more needs to be known about the homologies of the different chromosomes before cytological observations can help us to form a clearer idea of taxonomic relationships. In this connection, species of *Nectria* and *Hypomyces* which have imperfect stages other than *Fusarium* will have to be studied.

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EXPLANATION OF FIGURES

FIG. 1. A–F. Chromosome numbers in *Gibberella, Calonectria* and *Nectria* species. A. *Gibberella lateritium.* Third metaphase, 6 chromosomes in each nucleus. (About 3,200 ×.) B. *Gibberella roseum.* Diakinesis, 6 chromosome pairs. (About 2,000 ×.) C. *Calonectria rigidiuscula.* Diakinesis, 7 chromosome pairs. (About 3,000 ×.) D. *Nectria episphaeria* f. *coccophila.* Second metaphase, 7 chromosomes. (About 2,600 ×.) E. *Hypomyces solani* f. *cucurbitae,* cross between two hermaphroditic strains. Second interphase, 4 chromosomes in each nucleus. (About 1,800 ×.) F. *H. solani,* homothallic form. Diakinesis, 6 chromosome pairs. (About 2,500 ×.)

FIG. 2. A–F. Interpretation of chromosome content of nuclei shown in figure 1. A. *Gibberella lateritium,* 6 chromosomes. B. *G. roseum,* 6 chromosome pairs. C. *Calonectria rigidiuscula,* 7 chromosome pairs. D. *Nectria episphaeria* f. *coccophila,* 7 chromosomes. E. *Hypomyces solani* f. *cucurbitae,* 4 chromosomes. F. *H. solani,* 6 chromosome pairs.

AN UNDESCRIBED SPECIES OF PERICONIA

C. L. Lefebvre, A. G. Johnson, and Helen S. Sherwin [1]

(with 1 figure)

In September 1947, the senior writer collected at Garden City, Kansas, a plant of Colby milo that showed the characteristic symptoms of milo disease caused by *Periconia circinata* (Mang.) Sacc. as described by Leukel.[2] The following October, portions of the diseased roots of the above milo plant were placed in a petri-dish moist chamber for observation. After a few days, the characteristic *P. circinata* was evident at a number of points (fig. 1, A). In addition, another somewhat similar fungus, very evidently a species of *Periconia*, was noticed, in some cases coming from the same rootlets that showed *P. circinata*. The conidiophores, however, were erect instead of being circinate as in *P. circinata*, and the conidia, although they were globose, were distinctly larger and their surfaces were very much rougher than those of *P. circinata* (fig. 1, B–E).

Subsequently, single-spore cultures were made of the unidentified fungus and these were used in a soil inoculation experiment to test the pathogenicity of the fungus in comparison with *P. circinata*. Sand-cornmeal cultures of each fungus were mixed separately at two rates (16 oz. and 32 oz. per flat) with sterile soil and each lot of inoculated soil was placed in a different flat, 12 × 24 × 3 inches. Two additional flats were filled with similar sterile soil for controls. To one of these, 16 oz. of the sterile medium was added, and to the other, 32 oz. Seed of susceptible and resistant Colby milos, as

[1] The writers acknowledge with thanks the assistance of Miss Edith K. Cash in preparing the Latin description.

[2] Leukel, R. W. *Periconia circinata* and its relation to milo disease. Jour. Agr. Res. **77**: 201–222. 1948. *Illus.*

well as certain other grasses,[3] was sown in rows in all six flats and the flats kept in a warm greenhouse.

Periconia circinata attacked the susceptible but not the resistant milo, the same as reported by Leukel,[4] while the other grasses were not attacked. After six weeks, in the soil inoculated at both rates with *P. circinata*, the susceptible milo plants ranged from 1 to 2 inches high while those of the resistant milo ranged from 20 to 21 inches. The plants of both the susceptible and the resistant milos in the control flats averaged about 20 inches high.

The unidentified species of *Periconia* attacked neither of the milos nor any of the other grasses. In the soil inoculated at both rates with the unidentified species of *Periconia*, the plants of both the susceptible and resistant milos averaged about 20 inches high and were comparable with the controls in vigor and color.

It is evident, therefore, that the unidentified species of *Periconia* differs both morphologically and pathogenically from *P. circinata*. It likewise differs distinctly from the rough, globose-spored species of *Periconia*, listed by Linder.[5] It differs distinctly also from *P. heveae* Stevenson and Imle[6] in a number of respects, particularly in the prominent, conical spines or papillae on the walls of the conidia. Because of these various differences, the above unidentified species of *Periconia* is here proposed as:

Periconia macrospinosa Lefebvre et A. G. Johnson sp. nov.

Conidiophoris simplicibus vel apice sparse ramosis, rectis vel subflexuosis, totis atro-brunneis, 1–4-septatis (in cultura usque 11-septatis), usque circa 350 μ longis (in cultura longioribus), apud basim 10–11 μ in diam., supra 8–9 μ, cellulis basalibus et apicalibus paulo inflatis; *cellulis primariis sporogenis* pallide brunneis, forma variabilibus, 5–8 × 8–13 μ, circa cellulam apicalem verticellatis; *cellulis secondariis sporogenis* pallide brunneis, sphericis

[3] *Agropyron cristatum* (L.) Gaertn., *Andropogon scoparius* Michx., *Bouteloua curtipendula* (Michx.) Torr., *B. gracilis* (H.B.K.) Lag., *Buchloë dactyloides* (Nutt.) Engelm., *Eragrostis curvula* (Schrad.) Nees, *E. trichodes* (Nutt.) Wood, *Panicum antidotale* Retz., *P. virgatum* L., and *Stipa viridula* Trin.

[4] Loc. cit.

[5] Linder, David H. New Venezuelan Fungi Imperfecti. Mycologia **29**: 656–664. 1937. *Illus.*

[6] Stevenson, J. A., and Imle, E. P. *Periconia* blight of *Hevea*. Mycologia **37**: 576–581. 1945. *Illus.*

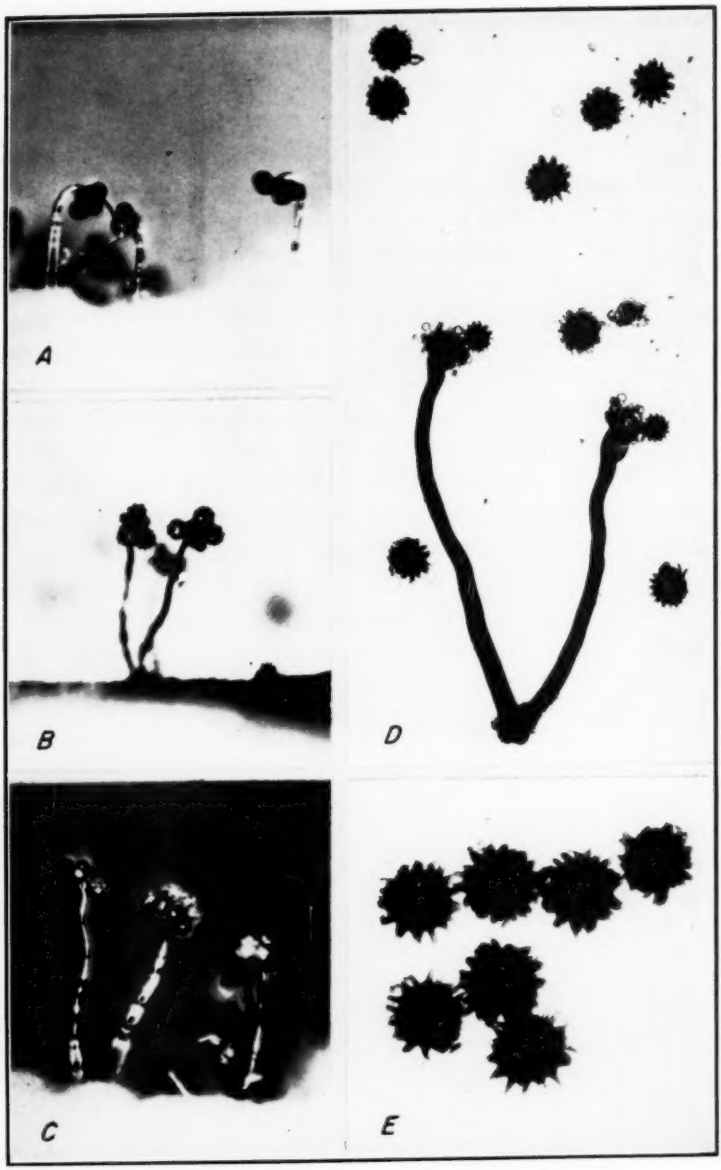

FIG. 1. *Periconia circinata* and *P. macrospinosa*.

usque late ovoideis, inconspicue verruculosis, 5–8 × 6–8 μ, in cellulis sporogenis primariis vel in cellula apicali conidiophori supra verticellum cellularum primariarum sporogenarum productis; *conidiis* atrobrunneis, sphericis, crasse spinosis, 18–32 μ, singulatim vel in catenulis brevibus fragilibus in cellulis secondariis sporogenis oriundis; *spinis* atro-brunneis, circa conicis, paulo deciduis, 2.5–6 μ altis, basi 2–3 μ in diam.

In radicibus emortuis *Sorghi vulgaris*, Garden City, Kansas, U. S. A.

Conidiophores simple or sparsely branched at tip, straight or slightly flexuose, dark brown throughout, 1–4-septate (up to 11-septate in culture), up to about 350 μ long (longer in culture), 10 to 11 μ in diameter near base, 8 to 9 μ above, the basal and apical cells somewhat enlarged; primary sporogenous cells light brown, variable in shape, 5–8 × 8–13 μ, forming a whorl about the apical cell; the secondary sporogenous cells light brown, spherical to broadly ovoid, inconspicuously verruculose, 5–8 × 6–8 μ, produced on the primary sporogenous cells or on the apical cell of the conidiophore above the whorl of primary sporogenous cells; conidia dark brown to black, spherical, coarsely spinose, 18–32 μ, borne singly or in short, fragile chains on the secondary sporogenous cells; spines dark brown, approximately conical, somewhat deciduous, 2.5–6 μ high, 2–3 μ in diameter at base.

On dead roots of *Sorghum vulgare* Pers. var. Colby milo, culture from specimen collected by C. L. Lefebvre, Garden City, Kansas, September 25, 1947 (**type**), deposited in the Mycological Collections of the Bureau of Plant Industry, Beltsville, Maryland, and in the Farlow Herbarium, Harvard University, Cambridge, Massachusetts.

BUREAU OF PLANT INDUSTRY STATION,
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EXPLANATION OF FIGURES

FIG. 1. A, *Periconia circinata* showing circinate conidiophores and dark-colored conidia, × 120. B–E, *P. macrospinosa*: B and C, straight to slightly flexuose conidiophores and dark-colored conidia, × 120; D, conidiophores, spinose conidia, two detached secondary sporogenous cells (near top), and detached spines, × 250; E, spinose conidia, × 500. (A and C, photographed chiefly by reflected light, others chiefly or entirely by transmitted light.)

A CYTOLOGICAL STUDY OF TYPICAL AND ATYPICAL BASIDIAL DEVELOPMENT IN GYMNOSPORANGIUM CLAVIPES

LINDSAY S. OLIVE

(WITH 14 FIGURES)

In an earlier paper (**1941**), the writer described a procedure for germinating teliospores of *Gymnosporangium* on slides and killing and staining the material *in situ*. Heidenhain's haematoxylin was used to stain the nuclei. With this method, distinct black nuclei are observed against a light cytoplasmic background. Although the technique does not bring out details of nuclear structure, certain other important features may be observed, such as the numbers of nuclei in basidial cells and basidiospores, nuclear divisions, and the appearance of the nuclei during migration.

Recently, a graduate student of this department, Mr. Robert Carroll, observed during a study of some slides of *G. clavipes* prepared by the writer that one or two of the basidiospores which he encountered were quadrinucleate instead of binucleate and that these spores were somewhat larger than the normal binucleate ones. This led to the present study by the writer to determine how such spores are produced and what their significance in the life history of the rust might be.

The writer is very grateful to Dr. C. W. Edgerton for his invaluable assistance with the photographic work.

INVESTIGATIONS

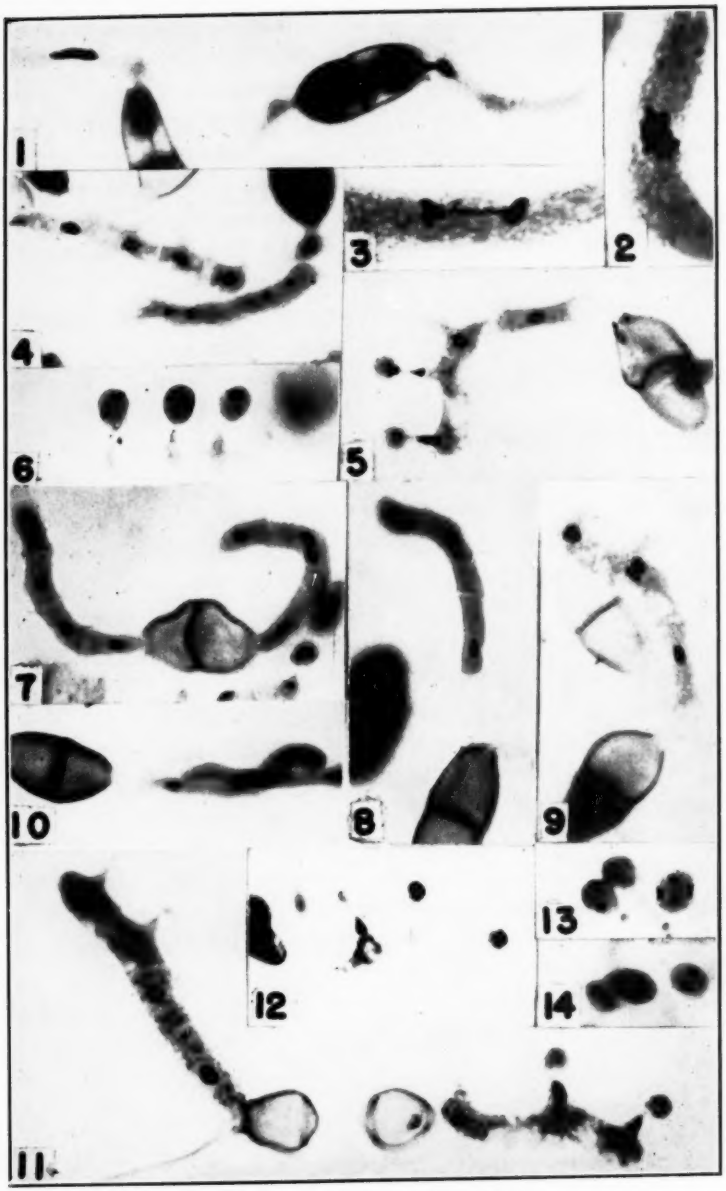
The reader is undoubtedly already familiar with the cytological details in the development of a typical rust basidium. Nevertheless, for the purpose of comparison with atypical developments, the process will be briefly reviewed here.

The teliospores of *G. clavipes* are two-celled and each cell, upon germination, produces a basidium. The basidium is produced

through a pore in the wall at the end of the teliospore cell. A portion of the cytoplasm passes out into the developing basidium and then the nucleus enters, becoming elongated and somewhat constricted as it passes through the region of the pore (FIG. 1). Eventually, the entire protoplasmic contents enter the young basidium, leaving the teliospore cell empty. The nucleus retains its elongated form (FIG. 1) and soon undergoes the first of the two divisions which are characteristic of basidial development. These are considered to be meiotic divisions.

With the present technique the prophase nuclei are generally stained a solid black (FIG. 1) and it is therefore impossible to distinguish the prophase chromosomes. However, during actual nuclear division, a distinct spindle and partially outlined chromosomes may frequently be observed (FIGS. 2, 3). The interphase between the first and second meiotic divisions is very short and the daughter nuclei enter almost immediately into the second division (FIG. 4). At this point, it is most important to observe the timing between cross wall formation and nuclear division. The first cross wall does not generally begin to appear until the second meiotic division is in progress. Occasionally it is not evident until after the second division has been completed. The septum appears about midway across the basidium. This is quickly followed by the appearance of a septum between the components of each pair of daughter nuclei of the second meiotic division, and a four-celled, four-nucleate basidium is produced (FIGS. 4, 7).

The basidium now enters into the final phase of development—the production of the basidiospores. Each cell gives rise to a sterigma which becomes quite pointed at its distal end. This pointed tip then expands into a subglobose structure which is the developing basidiospore. The cytoplasm and nucleus migrate through the sterigma into the swelling, the nucleus becoming much constricted as it passes through the attenuated portion of the sterigma (FIG. 5). Very soon after the nucleus has entered the developing basidiospore, it undergoes a mitotic division, the third in this series of nuclear divisions, and a binucleate basidiospore is produced (FIG. 6). This division is generally completed even before all of the cytoplasm has passed through the sterigma into the spore. The basidiospore is



FIGS. 1–14. *Gymnosporangium clavipes.*

discharged in the binucleate condition. Each basidium produces four binucleate basidiospores. The spores are not all to be found at the same stage of development on any one basidium. Frequently all stages of development may be observed on the same basidium. Generally the basidial cell nearest the teliospore is the last to produce a basidiospore.

Not all of the basidia of this rust are four-celled. A small proportion of them are three-celled. In such atypical basidia one cell contains two nuclei and each of the other two cells contains a single nucleus. The explanation for the occurrence of such basidia is to be found in a study of the relationship of cross wall formation to nuclear division. In most cases it is the middle cell of the three-celled basidium which is binucleate (FIGS. 7–9, 11). It has already been pointed out above that in the normal course of events the first cross wall in the basidium does not generally appear until the second meiotic division is in progress, or occasionally not until the division has been completed. In a few cases the first septum fails altogether to appear, while the two second division septa develop normally. This produces a basidium with a uninucleate cell at each end and a binucleate cell in the middle. Furthermore, the middle cell contains a nucleus from each of the second division spindles. There is no overlapping of spindles in the basidium.

Very rarely a three-celled basidium is found in which either the proximal or the distal cell is binucleate and the other two are uninucleate (FIGS. 10, 12). Two basidia of each type were observed during this study. In such basidia as these, it is apparent that the first septum developed normally, but one of the two second division septa must have failed to appear. The binucleate cell in such a basidium would obviously contain a pair of daughter nuclei derived from a spindle of the second meiotic division.

The three-celled basidium continues its development by producing three basidiospores instead of four. Each uninucleate cell gives rise to a normal basidiospore, while the binucleate cell gives rise to a basidiospore into which both nuclei migrate (FIGS. 11, 12). These two nuclei then undergo a mitotic division and a quadrinucleate basidiospore is produced (FIGS. 13, 14). These quadrinucleate basidiospores are conspicuously larger than the normal binucleate ones, as the photographs show.

An attempt was made to determine approximately what percentage of the mature basidia are three-celled. Well over a thousand basidia were examined to obtain this estimate. From this study it appears that about 0.75 per cent of the basidia are of the three-celled type.

DISCUSSION

There occur in the literature on rust cytology several references to certain rusts which normally produce basidia with one or more binucleate cells, and these cells produce basidiospores that are binucleate at their origin. Lindfors (**1924**) studied a race of *Puccinia arenariae* which produces two-celled basidia that give rise to two binucleate basidiospores. These spores in turn produce binucleate mycelia upon infecting the host. Thirumalachar (**1945**) found in *Cystopsora oleae* two types of basidia—one, the typical four-celled basidium, and the other, a two-celled basidium with binucleate cells. The two-celled basidium produces two binucleate spores. Thirumalachar further claims that the "diplophase" (dikaryophase) is initiated in the basidiospore and that the basidiospore, upon infection of the host, gives rise to a "diploid" (dikaryotic) mycelium. This concept is probably correct, although verification with experiments in monosporidial infection is needed.

Recently the writer (**1947**), in a cytological study of basidial development in *Sphenospora kevorkianii,* found that this rust typically produces three-celled basidia. One of the cells, usually the middle one, is binucleate and produces a binucleate basidiospore. The other two cells, which are uninucleate, produce uninucleate basidiospores. It is considered likely that the binucleate spores, at least in the majority of cases, are heterokaryotic, but verification of this is lacking.

In *Gymnosporangium clavipes,* the basidium is normally four-celled and produces four basidiospores that are uninucleate at their origin. However, a mitotic division occurs just before the spore is discharged so that each spore normally contains two nuclei at maturity. Such a condition is common in the rusts and many other heterobasidiomycetes and it does not mean that the spore is heterokaryotic. On the contrary, these two nuclei are probably genetically

alike. The basidiospore produced by the binucleate cell of the atypical basidium, however, is binucleate at its origin and becomes four-nucleate by a mitotic division of each nucleus before spore discharge. It seems likely that the majority of these spores are heterokaryotic. It is now generally acknowledged that segregation of factors may occur in both meiotic divisions in the basidium. If segregation of compatibility factors should occur in the first division, then the central binucleate cell, which receives a nucleus from each of the second division spindles, would be heterokaryotic for the compatibility factors. If segregation of these factors occurs in the second meiotic division, the spore has an equal chance of being heterokaryotic or homokaryotic for the compatibility factors.

Infection experiments with these atypical basidiospores should prove quite interesting. Although, in *G. clavipes*, the percentage of such spores is small, they could probably be distinguished in nature from the binucleate spores by their larger size. Also it should be possible to locate some of the three-celled basidia before they discharge their spores. One might suspect that the atypical spore would be capable of infecting the rosaceous host and could produce a dikaryotic mycelium that would give rise to aecia. Of course there is the other possibility, less likely, that the spore might infect the gymnosperm host, *Juniperus virginiana*.

A careful study of other species of rusts which normally produce four-celled basidia would probably reveal the presence of a certain percentage of these atypical basidia and basidiospores. There is some indirect evidence in the literature which lends support to this belief. There are numbers of instances in which an investigator, while working with monosporidial infections in heterothallic rusts, has occasionally obtained an infection which produced aecia. In several cases such results have been marked off to poor technique or to contaminations. In other instances the investigator has suggested that the dikaryon may have arisen spontaneously in the mycelium within the host. In view of the present findings, the writer believes that such results may have been obtained, in a number of cases, through the use of heterokaryotic basidiospores. Further investigations are needed to determine if this theory is correct.

SUMMARY

In *Gymnosporangium clavipes* the basidia are normally four-celled and four-nucleate and each cell gives rise to a basidiospore which is uninucleate at its origin, but becomes binucleate before discharge by means of a mitotic division of its nucleus. A small percentage of the basidia are three-celled. One of the cells of the atypical basidium is binucleate and the other two are uninucleate. The binucleate cell gives rise to a basidiospore which is at first binucleate but which becomes four-nucleate as a result of mitotic divisions. The four-nucleate basidiospore is believed to be in the majority of cases heterokaryotic. The possible role of this type of spore in the life cycle of the rust is discussed.

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Thirumalachar, M. J. Development of spore-forms and the nuclear cycle in the autoecious opsis rust, *Cystopsora olcae*. Bot. Gaz. **107**: 74–86. 1945.

EXPLANATION OF FIGURES

FIGS. 1–14. *Gymnosporangium clavipes*. 1, migration of the fusion nucleus into the developing basidium; 2, anaphase of the first meiotic division; 3, telophase of first division; 4, two basidia, one showing telophase spindles of the second meiotic division, the other being a mature 4-celled basidium which is producing sterigmata; 5, normal 4-celled basidium producing basidiospores; 6, basidiospores showing stages in nuclear division before spore discharge; 7, teliospore with normal 4-celled basidium and atypical 3-celled basidium, the latter with the middle cell binucleate; 8, 9, two 3-celled basidia, each with a binucleate cell in the center; 10, a 3-celled basidium with terminal cell binucleate; 11, teliospore with a 4-celled and a 3-celled basidium, the latter producing basidiospores; 12, a 3-celled basidium with the proximal cell binucleate, basidiospores developing; 13, 14, binucleate and 4-nucleate basidiospores. (All photographs approximately × 500, except 2 and 3 × 1,175.)

THE TAXONOMY OF SEPTOBASIDIUM POLYPODII AND S. ALBUM

J. N. Couch

(WITH 25 FIGURES)

Several members of the Auriculariales have been described as parasitic on mosses and ferns. These belong in the genera *Jola*, *Eocronartium*, and *Herpobasidium*, the first two occurring on mosses and the last on a fern. In 1929 the writer described as *Septobasidium Polypodii* a new fungus parasitic on the sori of *Polypodium* sp. Since the vegetative structure was not too unlike that of certain species of *Septobasidium* and the probasidia and basidia were quite similar to those of that genus, it was classified as a *Septobasidium* in spite of the absence of scale insects beneath the stroma. Later studies by Boedijn and Steinmann (**1931**) and the writer (**1938**) have shown that all species of *Septobasidium* live with scale insects. On the basis of this very distinctive feature, *S. Polypodii* has been excluded from the genus *Septobasidium*. In 1939 the late Dr. Linder sent me a fungus which was growing as a parasite on the lower side of the leaflets of a fern. The resupinate habit, the probasidia and thrice-septate basidia suggested a relationship with the fungus formerly described as *Septobasidium Polypodii*. It is the object of this paper to give descriptions of these two species on ferns, to discuss their taxonomic positions, and also to present new observations on *Septobasidium album*, showing that it should be transferred to the genus *Helicogloea*.

The two species on fern would seem to be distinct enough from *Jola* and *Eocronartium* on mosses and from *Herpobasidium* on fern to justify the establishment of a new genus. Since the fruit body is flattened it is being called *Platycarpa*.

Platycarpa gen. nov.

Fructificatio resupinata, minima sicca vel subcartilaginea, facile separabilis ab hospite maturitate; hyphis non nodosis ad septa; hymenio levi; probasidiis

hyalinis, membranis incrassatis; basidiis cylindricis vel curvatis; sporis allantoideis.

Parasitica in foliis filicis; haustoriis robustis praesentibus vel absentibus.

Fruit body resupinate, very small, dry to subcartilaginous, easily separable from host at maturity; hyphae without clamp connections; hymenium smooth; probasidia hyaline with thickened walls; basidia cylindric or curved; spores bent-ellipsoid.

Parasitic on fern leaves or sporophylls; with or without highly developed haustoria. Intermediate between *Septobasidium* and *Jola*. Distinguished by its occurrence on ferns, its small, flattened fruit body and the absence of scale insects. In its tenuous connection with its host, *Platycarpa* is quite like *Septobasidium;* but the host in the former is the fern and in the latter, scale insects.

Platycarpa Polypodii n. comb.

Septobasidium Polypodii Couch. Jour. Elisha Mitchell Sci. Soc. **44**: 255. 1929.

Resupinate, on the under surface of fertile fronds of *Polypodium* sp., parasitizing the sori and usually occurring in small patches up to 2 mm. wide, each patch limited to one fertile leaflet; sometimes the patches are confluent along the midrib of a sporophyll and then completely cover the lower surface for several centimeters; white when fresh, becoming cream-colored upon drying; in section 250–700 μ thick, usually about 500 μ thick, whitish throughout; composed of (1) a very thin lower layer of hyphae which extend over the lower surface of the fern leaf but do not penetrate into the epidermal tissue, and (2) a layer of compact, much-branched, coiled and entangled hyphae arising from the lower layer, often stratose by the successive formation of two or three fruiting regions; hyphae of context 3.8–5.4 μ thick, thick-walled, with inconspicuous septa spaced at irregular intervals, hyphae breaking up into short segments when crushed gently under a cover glass, noticeably constricted at the base of branches; probasidia formed near the outer surface of the compact layer, oval, 12.5–14.8 $\times$ 16–23 μ, wall slightly thickened, sometimes thicker on one side, germinating into a 4-celled, curved basidium 8.2–12.6 $\times$ 50–70 μ, with sterigmata about 8 μ long, each cell forming a spore; spores bent-ellipsoid, 6.5–8.5 $\times$ 19–25 μ, becoming once-septate, germinating by repetition; haustoria in shape of irregular coils within prosporangial and sporangial cells of host.

For a comparison of this species with *P. boliviensis* see that species.

Specimens examined:

Jamaica: Blue Mountains, on *Polypodium* sp., W. R. Maxon, coll., June 1926. **Type** in University of North Carolina Herbarium, and distributed to several other herbaria as *Septobasidium Polypodii*.

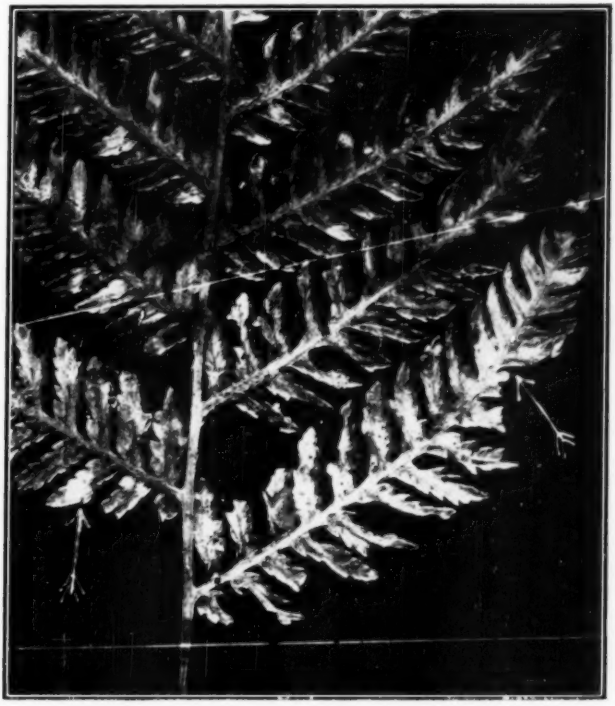


FIG. 1. Part of lower surface of dried fern leaf showing patches of *Platycarpa boliviensis*. These are usually lighter in color than leaf, as shown in small patches on left to which arrows point. On right, arrow points to area where fungus covers several leaflets. × 2.

Platycarpa boliviensis n. sp.

Fructificatio resupinata, hypophylla, plerumque orbiculata, facile separabilis, circa 1–2 mm. lata, interdum extensa secundum mediam venam ad 10 mm.; 0.2–0.8 mm. crassa si humida; immatura fulva, matura argillacea vel fusca, partibus vetustis humidis cartilagineis; haustoriis incompositis massis in cellulis epidermidis et mesophyllis; hyphis laxe intertextis, ascendentibus,

hyalinis, rare septatis, ramosis, 4–5 μ in diametro; hymenio non valde distincto ex contexto; probasidiis pyriformibus, proliferatione interna, 16–25 × 25–30 μ, membranis leviter incrassatis, vacuis ex germinatione; basidiis deciduis, divisis in quatuor cellulas, cylindricis vel curvatis, 8–10.9 × 65–85 μ; sterigmatibus brevibus 6–10 μ; sporis 6.3–8.4 × 29–39 μ; hyphis hymenii inaequaliter curvatis, attenuatis, circa 2.2 μ in diametro.

Resupinate, hypophyllous, forming closely applied but very easily separable, thin (when dry), inconspicuous, somewhat circular or irregular patches, usually one patch to a leaflet, or sometimes covering the lower surface of several leaflets; circular patches 1 or 2 mm. wide, the larger patches extending along the veins for as much as 10 mm. Pale buff and pulverulent when young; clay colored or wood brown and glabrous when older and cartilaginous when wet. Loosely attached to the leaf by a comparatively few threads which penetrate through the epidermis and stomata and form very irregular masses of hyphae in the epidermal and mesophyll cells. In section 200–800 μ thick when moistened, composed of rather loosely entangled, hyaline hyphae which are rather sparingly septate and usually slightly constricted at the septa, non-nodose, twisted, thin- to rather thick-walled, branched and 4–5 μ thick. Hymenial region not sharply set off from the context. Probasidia hyaline, pyriform, 16–25 × 25–30 μ, walls slightly thicker than hyphal walls, the basal part and also the supporting hypha crooked; renewed by internal proliferation, sometimes as many as four old walls and a new probasidium on the end of the same stalk; germinating and becoming empty to form the basidia, which are deciduous and apparently collapse readily. Basidia 4-celled, cylindrical or irregularly curved, 8–10.9 × 65–85 μ (only a few good ones seen). Sterigmata short, *i.e.*, about 6–10 μ. Spores hyaline, bent-ellipsoid, 6.3–8.4 × 29–39 μ. Hyphae of hymenium irregularly curved, the ends of uneven diameter, usually about 2.2 μ thick.

This fungus may be distinguished by its parasitism on the fertile leaves of a fern but not on the sporangia, by the very thin membranous appearance of the fructification when dry, the cartilaginous texture when wet, the hyaline, sparingly septate hyphae without clamp connections, the large, internally proliferating probasidia, the 4-celled, straight, or slightly curved basidia, and the large, bent-ellipsoid spores.

The nourishing hyphae of this species develop irregular masses chiefly in the mesophyll cells, being only occasionally found in the epidermis, and thus differing rather strikingly from *P. Polypodii*

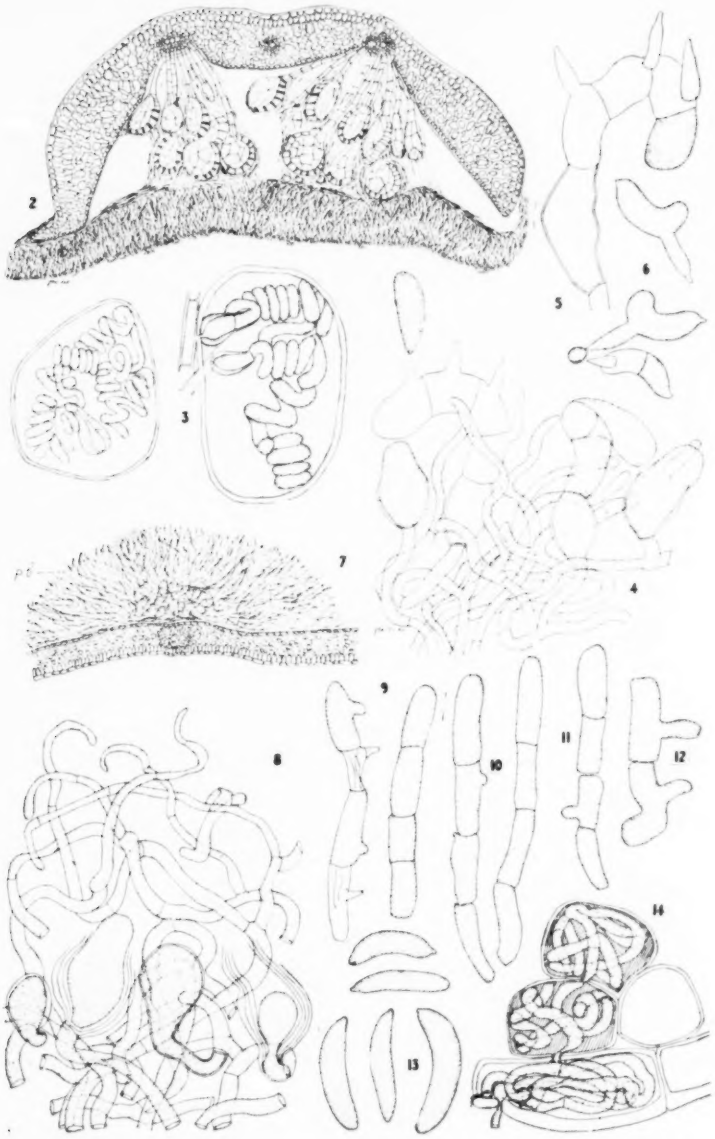
which has distinctly coiled haustoria within the cells of the very young sporangia. The two species also differ in texture and in the shape and size of the probasidia, basidia, and spores.

The early stages of infection have not been observed in either of the species of *Platycarpa*.

Specimens examined:

Bolivia: On fern sporophylls, H. H. Rusby, coll., sent by D. H. Linder. **Type** in Farlow Herbarium and University of North Carolina Herbarium.

Determining the relationships of the present genus offers considerable difficulty. At one time the writer (**1938**) suggested a relationship between *Platycarpa* (*Septobasidium*) *Polypodii* and the very peculiar genus *Goplana*, which is considered by Raciborski (**1900**) as intermediate between the Uredinales and Auriculariales. *Goplana* now seems to the writer to be closer to the former than to the latter order since its hymenium lacks hyphal tissue intermingled with the basidia. In *Platycarpa* the fructification consists of a comparatively large amount of sterile hyphal tissue, near the top surface of which is formed the hymenial layer composed of sterile hyphae, probasidia, and basidia, much as in certain species of *Septobasidium*. The present genus can be distinguished from *Septobasidium* by the invariable association of the latter with scale insects. Of all members of the Auriculariales it would seem to be closest to *Jola* and *Eocronartium*, both parasitic on mosses. *Jola* and *Platycarpa* can be distinguished by habitat, the former occurring on mosses, the latter on ferns. Also in *Jola* the probasidia are thin-walled and are formed in clusters, while in *Platycarpa* the probasidial walls are somewhat thickened and these structures are formed singly. *Eocronartium*, an obligate parasite on mosses, seems closely related to *Jola*, a suggestion further confirmed by the recent discovery by Stanley (**1940**) and others of probasidial cells in *Eocronartium*. This genus is readily distinguished from *Platycarpa* by the fact that the former occurs on mosses and by the probasidia and basidia. In *Eocronartium* (perhaps also *Jola*) the hyphae are thin-walled, much septate, and apparently only one kind of hypha is formed. In *Platycarpa* the hyphae are thin- to thick-



FIGS. 2–14. *Platycarpa Polypodii* and *P. boliviensis*.

walled with rather infrequent septations and the hyphal system is more complex. Another difference between the two is in the extent of the nourishing hyphae. In *Eocronartium* the hyphae extend through the stems and many of the leaves of the parasitized gametophytic thallus (Fitzpatrick, **1918**), while in *Platycarpa* the nourishing hyphae are quite limited in extent. The genus *Cystobasidium* was transferred to *Jola* by Patouillard (**1900**) but it seems best to me to follow Gäumann (**1922**) and treat it as a distinct genus. Both species of *Cystobasidium* have been reported as overgrowing other fungi, both lack hymenia, and both have clamp connections; all of these are characters which readily distinguish *Cystobasidium* from *Jola* and also from *Platycarpa*.

The genus *Herpobasidium* described by Lind (**1908**) and studied by Jackson (**1935**) occurs on ferns as an obligate systemic parasite and must be compared with *Platycarpa*. The following is taken largely from Lind and Jackson with some additional notes made from an abundance of dried material furnished me by Dr. Jackson. When mature the diseased areas show on the upper leaf surfaces as small brownish spots. On the under surface of such areas a white, mould-like growth is visible. Sections of these spots show abundant intercellular mycelium and conspicuous coiled intracellular haustoria, usually in the mesophyll but also in the epidermal cells. Branches from the intercellular mycelium emerge in fascicles through the stomata and these threads continue to branch and spread over the lower leaf surface, forming a very thin (8–34 μ thick) covering in the material examined by me. (Lind gave the thickness as 1 mm., width as 2 mm. and length as 4 mm.) The basidia arise from these horizontal hyphae, but in thin sections these hyphae are so sparse and inconspicuous that about all one can see are the basidia. As nearly as I could make out there are no sterile hyphae intermingled with the basidia in *Herpobasidium*, in sharp contrast to *Platycarpa* in which there is a fruit body composed of a relatively large amount of sterile tissue and relatively few probasidia and basidia. The coiled haustoria in *Herpobasidium* and in *Platycarpa Polypodii* are quite similar, but the striking differences in the fruit bodies in these two genera would serve easily to distinguish between them.

According to Jackson: "It is perhaps unimportant whether one considers *Herpobasidium* a member of the Auriculariales or a simplified form of the Uredinales. In any case it serves to emphasize the probable close relationship between the two groups." *Platycarpa* occupies an intermediate position between the Septobasidiales and the Auriculariales similar to that of *Herpobasidium* between the latter order and the rusts.

It seems that *Platycarpa* occupies a rather significant position in the evolution of such a highly specialized order as the Septobasidiales. In the Uredinales the most primitive genera grow on ferns. In the Septobasidiales no species has yet been found growing on ferns, but it is probable that *Platycarpa* might represent a sort of ancestral type of this order. At any rate, *Platycarpa,* which so strikingly resembles *Septobasidium* and is excluded from that genus only because of the fact that it is not associated with scale insects, furnishes a good connection between the Auriculariales and the Septobasidiales.

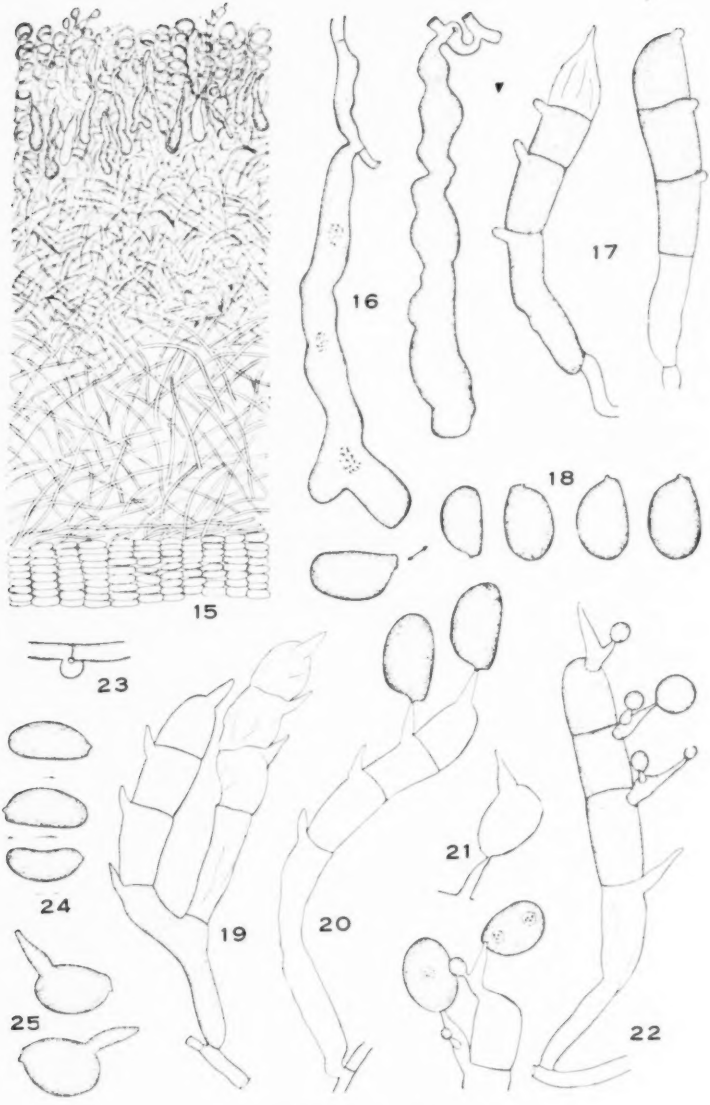
Uredinella, parasitic on scale insects, represents a similar transitional form between the Uredinales and the Septobasidiales, being close to *Septobasidium* in its association with scale insects and related to the rusts in that the "hymenial" layer in one species may be composed of a compact layer of teleutospores without sterile threads (Couch, **1937**) and thus is a true sorus. Indeed the teleutospores of *Uredinella coccidiophaga* are so much like those of certain species of *Uromyces* (*e.g., U. Fabae*) that it is difficult to know whether *Uredinella* should be in the Uredinales or in the Septobasidiales. Thus we find rather striking interconnections between these three orders: *Jola* and *Platycarpa* connect the Auriculariales and the Septobasidiales; *Herpobasidium, Goplana,* and other genera represent intermediates between the Auriculariales and the Uredinales; while *Uredinella* is intermediate between the Septobasidiales and the Uredinales. In spite of the fact that these orders are so obviously interconnected it would seem unwise to merge them into one or two at present. The Uredinales comprise a highly specialized group of obligate parasites which have for the most part a rather poorly developed vegetative mycelium but through "chemical stimulators" have put their hosts to work for them in the accumulation

of food for reproductive purposes. The Septobasidiales represent a parallel and very highly specialized order living symbiotically with colonies of scale insects and parasitizing certain individuals. The vegetative or nourishing mycelium in this order is rather poorly developed but is exceedingly highly specialized, absorbing food material from the living parasitized insects. The Auriculariales, containing the Auriculariaceae and the Phleogenaceae, are made up of a hodgepodge of genera. Some of these are interrelated while others may not even belong in the Heterobasidiomycetes. All of these genera with the possible exception of *Herpobasidium* have a well-developed vegetative mycelium. The commonest, best known, and most typical genera in this order (*Auricularia, Helicogloea,* and *Platygloea*) have well-developed fruit bodies and are saprophytic except for one or two species which are facultative parasites. (The parasitic genera in this order are discussed by Fitzpatrick (**1918**).) Though no one has made a study of the vegetative mycelium in any of these saprophytic genera, it is very likely that in all of them the nourishing mycelium is quite extensive. In addition to the rather striking physiological distinctions between these three orders, which I have emphasized above, there are also morphological differences.

Helicogloea alba (Burt) n. comb.

Septobasidium album Burt (**1926**)

Resupinate, forming small, circular, white, firm patches 1–6 sq. cm. in area; margin sharply determinate; surface resembling kid, pulverulent under a lens, broken here and there by irregular cracks. In section 600–700 μ thick, whitish throughout, composed of two rather indistinctly differentiated regions, a lower and an upper, each of about equal thickness. The lower region composed of diagonally ascending, entangled, fairly compact hyphae which are about 4–5 μ thick, have rather thick walls and are furnished with conspicuous clamp connections at the septa. The upper part of the fungus is composed of hyphae which are much coiled, are very compactly arranged, and 2.8–3 μ thick. Hyphae throughout both regions rather sparingly septate and usually with clamp connections at each septum; at the upper surface of the fungus the ends of the hyphae spirally coiled. Probasidia arising from near the bases of these coiled hyphae, usually growing backward or diagonally away



FIGS. 15–23. *Helicogloea alba.*

from the surface of the fungus; formed in clusters on hyphae rich in protoplasm, 7–12 × 50–70 μ, elongated, club-shaped, thickest at the distal end, constricted at one or several places, straight or bent, sometimes forked, forming a discontinuous layer one to several hundred microns below the upper surface. Rarely the probasidia may grow toward the surface of the fungus. Basidia 8–10 × 37–50 μ, typically 3-celled, with a long stalk that often forms a sterigma and spore; basidia arising from the base of the probasidium or from the upper part of the "primordial cell" or rarely from the apex of the probasidium when it is directed upward in the hymenium; sterigmata arising from near the top of each cell, usually short, 5–8 μ long, sometimes forked into a long and a short branch, bearing respectively a large and a small spore; rarely two sterigmata of equal length may arise on the end of the apical cell of the basidium; spores hyaline, ovoid, 7–9 × 10–15 μ, slightly flattened on one side and with a truncated proximal end and a minute papilla to which the sterigma is attached; germinating by repetition.

This fungus was first described by Burt as a species of *Septobasidium* but was excluded from that genus by me (**1938**) because of the close association of *Septobasidium* with scale insects and its invariable habitat on living plants. The position of the present fungus has remained in doubt until this past fall when in the course of studies on a new and remarkable heterobasidiomycete I examined herbarium material of *Helicogloea* and found that the spores of *Septobasidium album* were like those of *Helicogloea*. The spores of this genus, as noted by Baker (**1946**), are very characteristic. They are typically ovoid to ellipsoid and usually flattened on one side and have a prominent blunt protuberance at the proximal end. The small papillate mucro which is attached to the sterigma is at the edge of the truncation away from the flattened side of the spore (FIGS. 18, 24, 25). Further studies, particularly of sectioned material, showed the much-elongated probasidial sacs from which the basidia arose. Great difficulties were encountered in interpreting the probasidial structures. This was due to the fact that the first material studied was teased apart instead of sectioned and I mistook the irregular probasidia for basidia. It was only after a study of sectioned material which showed the large probasidia with their broader ends directed away from the surface that the relationship between the two structures was partly understood. It was noted further that the probasidia are very irregular in shape, whereas

the basidia are always nearly straight-cylindrical. Material teased apart in 7 per cent KOH, washed and then lightly stained with cotton blue or weak gentian violet and studied immediately, helped in showing a connection between probasidial cells and basidia. The probasidia collapse after they become empty and the usually long and twisted hypha or stalk between the probasidium and the basidium empties into the latter; hence this connection is difficult to follow. Several examples were found in teased material where the empty and partly collapsed probasidium was connected with a partly collapsed basidium. Typical probasidia are shown in figure 16. These are shown hanging downward. They are really growing away from the surface of the hymenium and are pendulous only if the fungus is growing on the upper surface of the substratum, which I strongly suspect it seldom does, and hence the probasidia would usually have the growing (larger) end directed upward (see Boedijn, **1937**). In figure 15 the probasidia are shown with their growing points directed away from the surface. This sketch was made from a comparatively thin and young section. In sections of older plants the probasidia are sunken deeper in the tissue and the region of coiled hyphae is considerably thicker. On the far left of the same figure is shown a probasidium germinating at its base to form a basidium initial which is growing toward the surface. The third (from the left) probasidium is empty and partly collapsed and is indistinctly connected by dotted lines to an empty and collapsed basidium. Left of this collapsed basidium is one with spores attached which apparently arose from a probasidium with its growing end directed toward the surface. Third from the far right is a basidium full of protoplasm, connected indistinctly to an empty probasidium.

The probasidia in this genus are furnished with walls so thin that the wall would perhaps serve little or no protective purpose against desiccation. The lack of a thick protective wall is compensated for by the sinking of the probasidia into the tissue. This reaches an extreme in *H. indica* where the probasidia are located near the base of the fructification (Boedijn, **1937**).

Baker (**1946**) points out that the species of this genus fall into two groups, one with a mucous-gelatinous fructification, the other floccose or hypochnoid. The present species is closer to the floc-

cose type but is much more like a *Corticium*, resembling *C. portentosum*, as mentioned by Burt.

Helicogloea alba agrees rather closely with *H. contorta* Baker in the size and color of the fructification, in the structure of the hyphae of the context, particularly in the spirally coiled hyphae near the outer surface, and in the size and shape of the probasidia, basidia, and spores. The two seem to differ in texture, *H. contorta* being floccose while *H. alba* is *Corticium*-like and rather firm and tough.

Specimens examined: New Zealand: Queenstown, Otago. On fallen branches of *Nothofagus*, December 3, 1919. G. H. Cunningham, coll. No. 542, **type**. Part of type in Mo. Bot. Gard. Herb.; U. S. D. A. Herb.; and U. N. C. Herb.

SUMMARY

A new genus of the Auriculariales is described. It is named *Platycarpa* because of its flattened fruit body and is based on two species, both of which are parasitic on tropical ferns. One of these, *Platycarpa boliviensis*, is described here for the first time; *P. Polypodii*, previously described as a *Septobasidium*, is transferred to *Platycarpa* and is considered the type species of this new genus. *Platycarpa* is compared with *Jola* and *Eocronartium* on mosses and *Herpobasidium* on ferns and shown to be distinct from each of these. The possibility that *Septobasidium* may have arisen from such a genus as *Platycarpa* is discussed.

The fungus described by Burt as *Septobasidium album* is transferred to the genus *Helicogloea* as *H. alba* because of the striking similarity in probasidial, basidial, and spore characters, as well as in the vegetative characters.

The writer is deeply grateful to H. S. Jackson, C. W. Dodge, John Stevenson, and G. H. Cunningham for the loan of herbarium material, and to Mrs. Alma H. Beers for inking most of the drawings.

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EXPLANATION OF FIGURES

FIG. 2. Diagrammatic section of fertile leaflet of *Polypodium* sp. showing section of fruit body of fungus, *Platycarpa Polypodii*, attached to sori. Hymenial region bearing probasidia, basidia, and spores, is on lower surface of fungus. × 22. FIG. 3. Two prosporangial cells of *Polypodium* sp. showing coiled haustoria of *P. Polypodii*. Disorganized contents of host cells not shown. × 543. FIG. 4. Section of hymenial layer of *Platycarpa Polypodii* showing sterile hyphae, probasidia, basidia, and spore. × 580. FIGS. 5, 6. Basidium and three spores of *P. Polypodii*. × 543. FIG. 7. Diagrammatic section of *Platycarpa boliviensis* showing part of fern leaf, context and probasidia (p.b.). Section made after soaking in 7 per cent KOH. × 22. FIG. 8. Section of hymenial region of *P. boliviensis* showing proliferating probasidia and curved threads of hymenium. × 500. FIGS. 9–13. Basidia and spores of *P. boliviensis*. × 500. FIG. 14. Part of section of lower epidermis and mesophyll cells of fern leaf showing nourishing hyphae of *P. boliviensis* within cells. Leaf first boiled in 7 per cent KOH for ten minutes before cutting section. × 860.

FIGS. 15–23, *Helicogloea alba;* fig. 24, *H. caroliniana;* fig. 25, *H. pinicola.* Fig. 15, × 192; fig. 23, × about 600; others, × 675. FIG. 15. Cross section of young fructification of *Helicogloea alba*, semi-diagrammatic. For explana-

tion see text. FIG. 16. Two probasidia. FIG. 17. Two basidia. FIG. 18. Five spores. FIG. 19. Two basidia attached to same branched probasidium(?). FIG. 20. Basidium with long stalk-cell. FIG. 21. Spore germinated by repetition attached to sterigma of basidium. FIG. 22. Basidia with branched sterigmata. FIG. 23. Clamp connection. FIG. 24. Spores of *H. caroliniana*, one of which is slightly bent-ellipsoid; others flattened on one side and showing truncated end with a little mucro. FIG. 25. Two spores of *H. pinicola* (Galzin No. 20555) germinating by repetition, both showing truncated proximal ends with small papillate mucros.

OXYPORUS NOBILISSIMUS AND THE GENUS OXYPORUS IN NORTH AMERICA

WM. BRIDGE COOKE

(WITH 10 FIGURES)

Attention has been called to the existence of this genus of pore fungi in North America by the discovery in 1943, and the subsequent collection between 1943 and 1948 at several locations in Oregon and Washington, of specimens of a most unusual species of "*Fomes.*"

In July, 1948, the writer visited the Botany Department at the University of Washington in Seattle and was shown and lent a portion of a large fungus which had been given to D. E. Stuntz. Several specimens collected by A. H. Smith and D. E. Stuntz (FIGS. 8–10) in Mount Rainier National Park intensified the writer's desire to know more about the specimen obtained in Seattle. A lead was available through Charles Gardner Shaw of the Department of Plant Pathology, Washington State College of Pullman, Washington. Through conversations, and later correspondence, with C. R. Allison, he learned of a giant "*Fomes*" collected in Lewis Co., Wash., which had been placed on display in the office of the Weyerhauser Lumber Co., Longview, Wash. It was discovered that other similar but smaller conks had been sent to L. O. Overholts by J. L. Bedwell of the Portland Office of the Division of Forest Pathology, Bureau of Plant Industry, Soils and Agricultural Engineering, U. S. Dept. of Agriculture. It became referred to facetiously by foresters who were acquainted with it as "*Fomes fuzzii-sandozii*" because of its fuzzy appearance and the fact that the first specimens found in Clackamas Co., Ore., in 1943, were collected by the brothers Ali and Fred Sandoz. In 1946, Jacob Hisey found a large specimen, one of the largest fungus fruit bodies known, in Lewis Co., Wash. It weighed at least 300 lbs. and measured 56×37 inches. At least, among

the polypores, this size may be equaled only by some exceptional conks of *Fomes officinalis*.

The following description of the genus *Oxyporus* was translated from Donk's (**8**) treatment of the Aphyllophoraceae of The Netherlands:

OXYPORUS (Bourd. & Galz.) Donk

Oxyporus (Bourd. & Galz.) Donk, Rev. II. Med. Bot. Mus. Utrecht, No. 9, p. 202. 1933.

Coriolus Sect. IV. *Oxyporus* Bourd. & Galz. Soc. Myc. Fr. Bul. **41**: 139. 1925.

Polyporus Fr., Syst. Myc. 1821. pr.p.

Fructification stalked, resupinate-reflexed or wholly resupinate, perennial. Pileus, when present, anoderm. Tubes at least two- to many-layered, rarely remaining one-layered; pores small, oval-rounded. Trama woolly-corky, somewhat fibrous, white or at most pale leather colored, occasionally strongly reduced.

Cystidia present, with a cap of calcium oxylate crystals on the apex. Spores ovate-rounded, smooth, hyaline, small (3.5–5 μ).

Upon wood.

Type: *Polyporus populinus* Fr.

All treatments of this genus studied to date list only one principal species, *Fomes connatus* or *F. populinus*, with a secondary species, *Poria obducens*, which is sometimes listed as a synonym, a subspecies, or a variety of *Fomes connatus*. Bondarzew and Singer (**2**) indicate the inclusion of *O. ravidus*, a non-stratose species not reported from North America, treated as a *Trametes* by Pilát (**19**).

Within the genus *Fomes* Kickx (**10**) there are several groups of species which seem to have little relationship to each other. Fries (**9**), followed later by Winter, Killermann and others, divided the genus into six or more sections, related to each other only by the presence of a tubular hymenium, perennial habit, and woody or near-woody structure. In the section "Laevigati" were placed species which were not rimose, did not have a crust, but whose surface was smooth. Into this section, then, fell the fungus referred to as *Fomes populinus* or *F. connatus*.

In splitting *Fomes*, Karsten erected *Fomitopsis* for species with white or light colored context and in this he is followed at present, to a certain extent, by Cunningham (**7**).

Murrill (**15**) retained *Fomes* for the light-context species. He used other generic categories for perennial *Fomes* with dark context and other characters.

Other workers in the United States including Overholts (**18**), Lowe (**14**), Baxter (**1**), Shope (**20**), Neuman (**16**) and others have used the genus *Fomes* in the sense in which it was used by Fries.

In 1925, Bourdot & Galzin (**3**) in France established a subgenus in the genus *Coriolus* for *Fomes connatus*. Quélet had already placed this species in that genus and Bourdot and Galzin set it apart from other species as the subgenus *Oxyporus*. In 1933, M. A. Donk (**8**) elevated *Oxyporus* to generic rank. He placed two common species in this genus: *Fomes connatus* and *Poria obducens*. Pilát (**19**) in Czechoslovakia, Imazeki (**11**) in Japan, Bondarzew and Singer (**2**) in Russia, and Singer in the revised Farlow Herbarium arrangement, have followed Donk in this although Bondarzew and Singer have indicated that they have emended the genus to include an acystidiate form of *C. obducens* and a non-stratose species, *O. ravidus*. Included with *Oxyporus* in the tribe *Oxyporeae*, Bondarzew and Singer place the genera *Baeostratoporus*, *Heteroporus* and *Irpex*.

KEY TO SPECIES

a. Pileus with a deep surface layer of interwoven fibers; on conifers; spores 6–7 × 3.5–4 μ ..... *O. nobilissimus*
a. Pileus with smooth to pubescent surface; on hardwoods; spores 3.5–4.5 × 3–4 μ ..... *O. populinus*

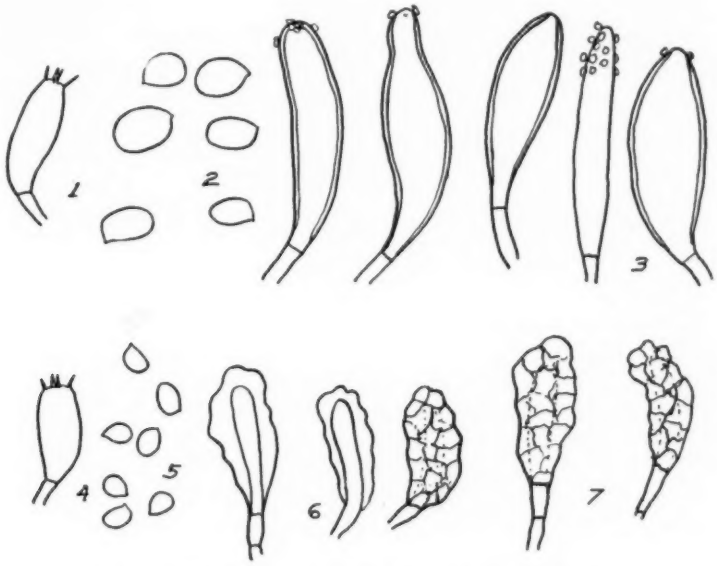
Oxyporus nobilissimus sp. nov. FIGS. 1–3, 8–10

Pilei dense strigosi, fibris ramosis hispidi, zonati, suberoso-lignosi, effuso-reflexi vel substipitati, sicutae imbricati, concrescentes, perenne, 30–140 × 25–95 × 30–100 cm., albi cinereive, intus poris stratosis, carne mediocri, 2–5 mm. crassa, dense fibrosa; margine obtuso, sterili; tubulis 2–7 mm. longis, ore rotundatis, in juventute albis, 400–500 μ diam.; hyphis longis, hyalinis, raro ramosis, non septato-nodosis; cystidiis hyalinis, capitatis, crystallinis, 15–23 × 3–6 μ; basidiis tetrasterigmaticis, 12–15 × 4–5 μ; sporis ellipsoideis, hyalinis, uniguttulatis, unicellularibus, 6–7 × 3.5–4 μ.

Hab. ad truncos *Tsugae heterophyllae*, Mt. Rainier National Park, Washington. Leg. A. H. Smith et D. E. Stuntz, A. H. Smith 31102. Sept. 9, 1948.

Pileus perennial, sessile, or centrally substipitate, ungulate, imbricate, massive, 30–140 × 25–95 × 30–100 cm., at least one speci-

men weighing as much as 300 lbs., distinctly stratified from each season's growth, with a thin layer of sterile tissue between successive trametoid tube layers. Color of old context more or less cinnamon-buff or more ochraceous, fresh growth white to sordid white and fibrous, texture when fresh semi-woody; surface of pileus a dense mat of white mycelial fibers composed of bundles of parallel, elongate, septate, thin- to slightly thick-walled hyphae; the bundles branch and anastomose freely and the fiber mat shows evidence of seasonally added increments of growth.



FIGS. 1–7. *Oxyporus nobilissimus* and *O. populinus*.

Hyphae of context flexuous, hyaline, 3–5 μ in diameter, walls thin to slightly thickened, of two types: generative hyphae terminating in the hymenium, thin-walled, flexuous, septate but not with clamp connections, intermingled with the thin- to slightly thick-walled interwoven skeletal hyphae which emerge from the upper surface of the pileus to form, in parallel arrangement, the mat fibers.

Tubes 2 per mm., white, round, 2–3 mm. deep in a new layer on a fresh specimen collected in September, 2–7 mm. deep in mature layers, averaging 5 mm. deep, not becoming stuffed; 35 seasons of growth counted in one of the Mt. Rainier specimens; in all specimens examined the youngest tube layer white and the tube trama trametoid in structure.

Cystidia hyaline, walls slightly thickened, apex with a crystalline cap, 15–23 × 3–6 μ. Basidia 4-spored, 12–15 × 4–5 μ. Spores 1-celled, hyaline, smooth, thin-walled, 6–7 × 3.5–4 μ.

Habitat: On *Abies procera* Rehder and *Tsuga heterophylla.*

Distribution: Clackamas Co., Oregon; Lewis Co. and Mt. Rainier National Park, Washington.

Type specimen: Collected by A. H. Smith and D. E. Stuntz, A. H. Smith No. 31102, on *Tsuga heterophylla,* Mt. Rainier National Park, Washington, Sept. 9, 1948. Portions of this specimen are filed in the Herbarium of the University of Michigan; the Mt. Rainier National Park Herbarium, the herbarium of the Univ. of Wash., Seattle, Wash., the herbarium of Wm. B. Cooke, and that of D. V. Baxter.

Important specimens: Collected by Jacob Hisey, July 13, 1946, on *Abies procera* at location 559, N.E. ¼ of S.E. ¼, Sec. 5, T. 11 N., R. 4 E., Lewis Co., Washington. Portions of this specimen are in the Herbarium, Dept. of Plant Pathology, State College of Washington, Pullman; Herbarium, University of Washington, Seattle; and the writer's herbarium. The main part of the specimen is on display in the office of the Weyerhauser Lumber Co., Longview, Wash.

To the writer's knowledge, the first specimens of this species were collected by Ali and Fred Sandoz on *Abies procera* on the Dwyer Brothers operation on the Mt. Hood National Forest in the Clackamas Drainage near Oregon City, Clackamas Co., Oregon, June 10 and July 10, 1943. These specimens were turned over to the Portland office of the Division of Forest Pathology where specimens are now filed and from whence specimens were sent to Dr. L. O. Overholts in whose herbarium at Pennsylvania State College two specimens are filed under the numbers 23909 and 24218. A portion of one specimen was also sent to the Forest Pathology Collections at Beltsville, Maryland.

These first specimens were found associated with living trees of *Abies procera* within 5–6 feet of their base, according to the Allison correspondence, within 3 feet of their base according to correspondence with J. L. Bedwell. Attempts to trace the fructifications to the nearby trees were unsuccessful and incomplete; felled trees were reported by Allison, in correspondence, to have shown no signs of infection. The specimens from Mt. Rainier seen by

Photo A. H. Smith.

FIG. 8. *Oxyporus nobilissimus*. ×⅓.

the writer are associated with a brown rot of lowland hemlock (*Tsuga heterophylla*).

C. G. Shaw at the Dept. of Plant Pathology, State College of Washington, attempted to make tissue cultures from one of the specimens collected on Mt. Rainier. The specimen was collected in September and the cultures were attempted without success in November.

Aside from the large size of most of the known conks of this fungus it has many interesting features which set it aside as distinct from all other known species of the genus *Fomes* and its segregates except *Oxyporus populinus* described below. Upon first glance one is struck by its similarity to this fungus, which grows only upon hardwood trees. The tubes are separated by layers of white tissue and the context is white (FIG. 10), but there the macroscopic similarity ends. Microscopically, both species have capitate incrusted cystidia in the hymenium (FIGS. 3, 6, 7).

The surface of the specimens of *O. nobilissimus* is covered with loosely interwoven, stiff, matted fibers giving the appearance (FIGS. 9–10), as suggested by A. H. Smith in his field notes, of some *Tremellodendron* species. The individual fibers of this mat are rounded to flattened. They are composed of elongate, hyaline, thin- to slightly thick-walled septate hyphae which are arranged parallel or somewhat interwoven but densely compacted. These hyphae do not have clamps, are not flexuous and are not gelatinous. The fibers which are made up of these long straight hyphae are 50–200 μ in diameter, and branch and anastomose freely. The mass of fibers originates from the context in which the hyphae which produce the fibers are densely interwoven with other hyphae. The fibers leave the context, with the hyphae which compose them, already in their parallel arrangement. These bundles of hyphae leave the context parallel to it, tangential to the cap surface, and are renewed at intervals (FIG. 10). These intervals may not correspond to the seasons of growth in which the tubes are renewed in additional layers but their effect is similar. Thus within this surface layer, which may be as much as 5 cm. deep, there may be a number of increments of this tissue distinguishable by white to light colored areas probably indicating areas of renewed growth in-

Photo A. H. Smith.

FIG. 9. *Oxyporus nobilissimus* (36 inches wide).

tensified at the start of a growing season. Where the many fibers appear perpendicular to the conk-surface (anticlinal rather than periclinal) this is probably caused by crowding through increasing growth, or realignment in older areas.

The context of the sterile tissue between the tube layers and above the oldest tube layer beneath the fiber mat is composed of densely interwoven hyphae which are hyaline, septate, not clamped, 3–4 μ in diameter. The context is trametoid, there is no distinction between the tube trama and the context. The sterile tissue between the tube layers is white and varies in thickness from 0.25 to 3.0 mm., but is mostly between 0.5 and 2 mm. (FIG. 10). This tissue is leathery to corky or woody. Between the tube layers and the fiber mat at the upper surface, the context is between 0.5 and 2 mm. thick.

In treating certain tropical polypores E. J. H. Corner (**4, 5**) developed a system of classification of tissues within the trama on the basis of the types of hyphae of which they were composed. This system was recently further elaborated and used as the basis for the systematic treatment of New Zealand polypores by G. H. Cunningham (**6**). According to this system of hyphal classification two hyphal types are represented in the Mt. Rainier specimens as well as in the Lewis Co. giant. The generative hyphae are those which produce the basidia and the cystidia. The greater part of the tissue of the conk is composed of skeletal hyphae. These hyphae are of Cunningham's "long type" and they are the hyphae which develop into the elongate fibers of the surface mat. Binding hyphae are not present so that this fungus represents a dimitic hyphal type without clamp connections. In Cunningham's classification (**7**) the fometoid fruit body with a dimitic hyphal system without clamp connections is characteristic of *Fomitopsis*. This concept represents an emendation of Karsten's original concept of this genus.

In the section devoted to cover tissues in Lohwag's "Anatomie" (**13**) there is no mention of a tissue such as the one on the surface of the conks of this fungus. Lohwag's cover tissues are all relatively simple ones and the hyphae of the different kinds of derms and cutis are relatively simple, not compound bodies such as the fibers of the mat described above. Study of other compound

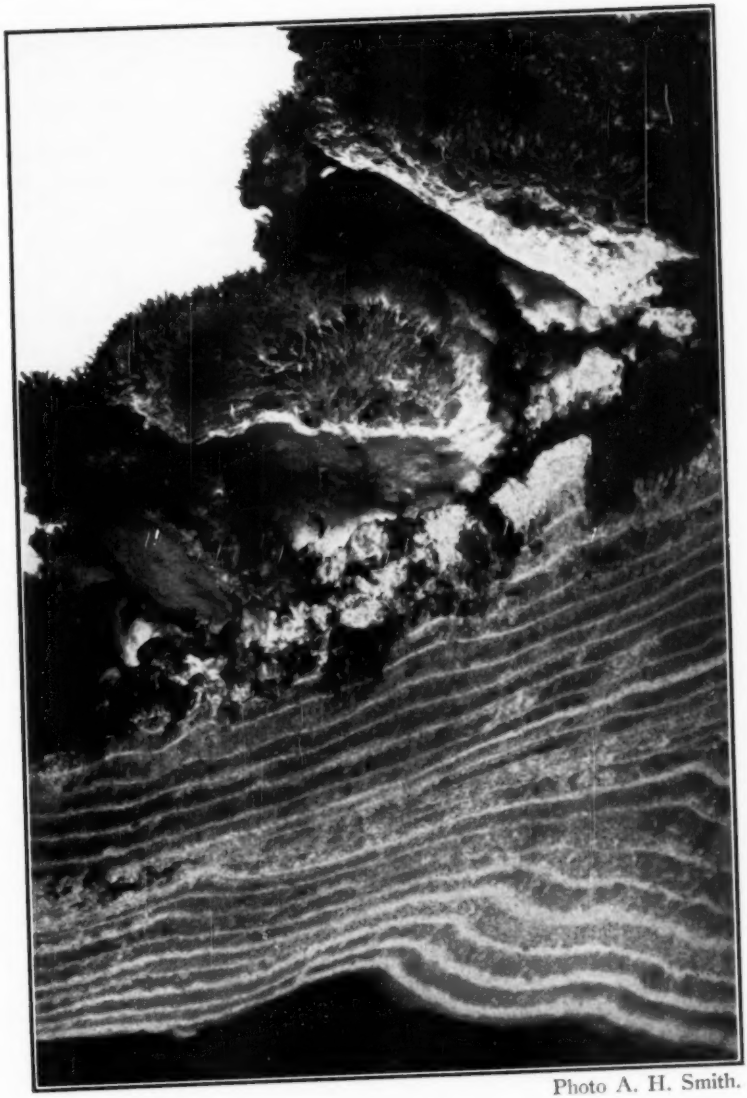


Photo A. H. Smith.

FIG. 10. *Oxyporus nobilissimus.* ×½.

trichoderms such as those of *Pogonomyces hydnoides, Funalia mons-veneris* and *Trametes hispidus* would be necessary in order to properly evaluate the cover tissue of this fungus.

Until recently *Oxyporus populinus* was the only fungus found in North America which could be assigned to this genus. No other species which had layers of white context between the layers of tubes was known to Lloyd in 1915 (**12**). Baxter (**1**), in 1948, says "there are no closely allied species." Overholts said, in part, in a letter to J. L. Bedwell dated June 30, 1943: "It appears to be a good species of *Fomes* of the white context group but the pileus covering is so different from any other *Fomes* that I am at a loss as to what to do with it. I have had nothing like it previously."

OXYPORUS POPULINUS (Fr.) Donk

Boletus populinus Schum., Saec. p. 384. 1803—"varietas videtur"—Fr.
Polyporus populinus Fr., Syst. Myc. **1**: 367. 1821.
Polyporus obducens Pers., Myc. Eur. **2**: 104. 1825.
Polyporus necsii var. *connatus* Weinm. ex Fr., El. **1**: 92. 1828.
Polyporus connatus (Fr.) Weinm., Fl. Ross. 332. 1836—non *Polyporus connatus* Schw., Am. Phil. Soc. Trans. ii. **4**: 154. 1832.
Fomes connatus Gill., Champ. Fr. **1**: 684. 1878.
Polyporus oxyporus Sauter, Hedw. **15**: 150. 1879.
Fomes populinus (Fr.) Cke., Grev. **14**: 20. 1885.
Fomitopsis connata Karst., Rev. Myc. **3**: 18. 1881.
Trametes connata Karst., Act. Fenn. **3**: 30. 1881.
Leptoporus connatus Quél., Ench. Fung. 177. 1886.
Poria obducens (Pers.) Quél., Ench. Fung. 180. 1886.
Coriolus connatus (Fr.) Quél., Fl. Myc. 391. 1888.
Physisporinus obducens (Pers.) Gillot & Lucand, Cat. Ch. Saone-et-Loire, 697. 1891.
Polyporus meliae Underw., Torr. Bot. Cl. Bul. **24**: 85. 1897.
Fomes meliae (Underw.) Murr., Torr. Bot. Cl. Bul. **30**: 232. 1903.
Fomes oxyporus Lloyd, Syn. Gen. Fomes, Myc. Writ. **4**: 283. 1915.
Polyporus cremeus Bres. ex Lloyd teste Bres., Ann. Myc. **18**: 67. 1920.
Polyporus ulmarius Velen., C.H. 661. 1922. (non Fr.)
Coriolus connatus ssp. *obducens* (Pers.) Bourd. & Galz., Soc. Myc. Fr. Bul. **41**: 137. 1925.
Oxyporus populinus Donk, Med. Bot. Mus. Utrecht **9**: 204. 1933.
Oxyporus obducens (Pers.) Donk, Med. Bot. Mus. Utrecht **9**: 202. 1933.
Oxyporus populinus var. *obducens* (Pers.) Pilát, Atlas des Champignons de l'Europe, III: 343. 1936–42.

Pileus perennial, sessile to resupinate, convex, imbricate, corky to woody, 2–10 × 3–15 × 0.5–4 cm.; surface white to yellowish,

sometimes becoming grayish black, often becoming covered with moss and algal growth, velvety tomentose to glabrous, not zonate, never rimose; margin thick, usually narrowly sterile below; context white or whitish, drying white to cream color, soft, spongy to nearly succulent when fresh, corky when dry, 0.3–4 cm., usually less than 2 cm., thick, the hyphae rarely branched, thin-walled, 2–5 μ in diameter, generative and skeletal hyphae densely interwoven; very similar to each other; tubes white or whitish, distinctly stratified, the layers of tubes separated from each other by a layer of context 0.5–1 mm. thick, 1–5 mm., mostly about 3 mm. long each season, mouths white to whitish or yellowish, often glistening, angular, averaging 4–5 per mm., the edges entire to slightly dentate, rather thin.

Cystidia present although not reported from all specimens, capitate or club-shaped, 11–19 × 3–7–11 μ in diameter, mostly appearing as crystalline bodies in the hymenium; basidia 7–9 × 4–5 μ; spores hyaline, smooth, sometimes 1-guttulate, ellipsoid to globose, 3.5–4.5 × 3–4 μ.

Habitat: Baxter and others list the following woody species as host to this fungus: *Acer dasycarpum* var. *lutescens*, *A. macrophyllum*, *A. negundo*, *A. rubrum*, *A. saccharinum*, *A. saccharophorum*, *Aesculus hippocastanum*, *A. octandra*, *Betula lutea*, *Carpinus caroliniana*, *Carya glabra*, *Carya* sp., *Cornus florida*, *Fagus grandifolia*, *Fraxinus americana*, *Gleditsia triacanthos*, *Halesia carolina*, *Liquidamber styraciflua*, *Melia azederach*, *Nyssa silvatica*, *Ostrya virginica*, *Quercus alba*, *Q. prinus*, *Sambucus* sp., *Ulmus americana* and *U. fulva*.

Within North America the following provinces and states are listed as areas within which this fungus has been collected: Canada: British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, Prince Edward Island and Quebec. United States: Alabama, Arkansas, Delaware, Illinois, Indiana, Kansas, Kentucky, Iowa, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, Pennsylvania, Rhode Island, South Dakota, Tennessee, Vermont, Virginia, West Virginia and Wisconsin. Pilát reports it from the following European countries: Czechoslovakia, Hungary, Germany, France, Norway, Sweden, Esthonia, Finland, Poland, The Netherlands, Jugoslavia, Latvia and Russia. M. C. Cooke reported it from Australia, according to Pilát.

Its pathology and activity in pure culture are adequately described by Baxter (**1**) and Nobles (**17**).

In its resupinate form it has been referred to as *Poria obducens* Pers. Workers in North America have usually considered this species as synonymous with *O. populinus* and we shall follow Lowe (**14**), Baxter (**1**), and others in this interpretation.

The above description of *O. nobilissimus* was drawn from field notes by A. H. Smith and laboratory notes by the writer. The description of *O. populinus* was drawn from several descriptions including those of Lowe (**14**), Donk (**8**), Baxter (**1**), Pilát (**19**), Bourdot and Galzin (**2**), and from notes by the writer. The synonymy of the latter species was drawn from Pilát (**19**), Donk (**8**), and Baxter (**1**). In addition to the above synonyms Pilát lists "*Polystictus populinus* var. *connatus* Fr., El. 92. 1825." This is an inaccurate citation since Fries did not raise *Polystictus* to generic rank until 1851 and the Elenchus was published in 1828. Host and location lists were obtained mostly from Baxter (**1**).

The writer wishes to take this opportunity to thank Donald P. Rogers for checking the Latin description of *Oxyporus nobilissimus;* A. H. Smith, D. V. Baxter and C. G. Shaw for reading the manuscript and offering valuable criticisms and suggestions; and A. H. Smith for use of his photographs of the Mount Rainier specimens.

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PULLMAN, WASH.

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DESCRIPTION OF FIGURES

FIGS. 1–3. *Oxyporus nobilissimus:* 1, basidium; 2, spores; 3, cystidia. FIGS. 4–7. *Oxyporus populinus:* 4, basidium; 5, spores; 6, cystidia in optical section; 7, cystidia showing incrustation.

FIG. 8. One year's growth of *Oxyporus nobilissimus* showing the tufted nature of the fibrils forming the covering of the pileus. × ⅓.

FIG. 9. Old fruiting body of *Oxyporus nobilissimus* showing growing margin and matted fibrils forming the covering of the pileus. The fruiting body measured about 36 inches across.

FIG. 10. Sectioned fruiting body of *Oxyporus nobilissimus* showing layer between the tube strata and rejuvenation from pileus surface. × ⅓.

SCHWEINITZ–FRIES LETTERS

C. L. Shear

(with 2 figures)

The following letters represent the only correspondence so far known between these two distinguished mycologists. As may be noted in the transcription of Fries' letter, he lists those decades of his Scler. Suec. sent to Schweinitz at that time, stating that the lacking numbers would follow. A check of the specimens from Fries in the Schweinitz herbarium, as represented in the Michener Collection, showed no specimens among those numbers which were to be sent at a later date. This would indicate that no additional specimens were received by Schweinitz and apparently no further correspondence ensued. No other letters have been found at Philadelphia or Uppsala.

The original Schweinitz' letter is preserved in the Botanical Institute of the University of Uppsala, Uppsala, Sweden. A photostat copy of this was provided through the courtesy of Dr. J. A. Nannfeldt and has been transcribed and translated by Dr. G. Steiner of the United States Plant Industry Station, Beltsville, Maryland. The copy of Fries' reply, which is at the Philadelphia Academy of Natural Sciences, was kindly supplied by Dr. F. W. Pennell of the Academy and translated by Miss Edith K. Cash of the Plant Industry Station. To all the above who have so kindly assisted in making the publication of these letters possible, we wish to express our gratitude.

Bethlehem, Northampton County,
Pennsylvania
17th Jany. 1823.

Hochgeehrter Herr

Die Güte meines Freundes Liliencron, dessen Gesellschaft ich schon über ein Jahr genossen, und der im Begriff ist in sein Vaterland zurückzukehren, verschafft mir die längst gewunschter Gelegenheit, zumal derselbe sich Ihrer persönlichen Bekanntschaft

erfreut, Ihnen schriftlich die Hochachtung zu begrüssen, welche mir Ihre unschatzbaren Arbeiten für mein Lieblings-studien die Mycologie einflössten, und es zu wagen Ihnen eine kleine Sendung von etlichen hundert Nord. Americ. Fungi in der Hoffnung zu übersenden, dass dieselben Ihnen angenehm sein werden. Eine beträchtlichen Theil derselben werden Sie in dem kleinem Werk finden, welches Dr. Schwägerichen in der Leipziger Gesellschaften Schrift von mir hat einrücken lassen. Die übrigen sind seitdem gefunden, und so viel ich weiss nur in meinen ungedruckten Papieren beschrieben. Wenn es Ihnen angenehm wäre würde ich im Stande sein Ihnen von den 1600 Species die ich bisher hier und an meinem früheren Wohnort in Nord Carolina beobachtet habe (von denen

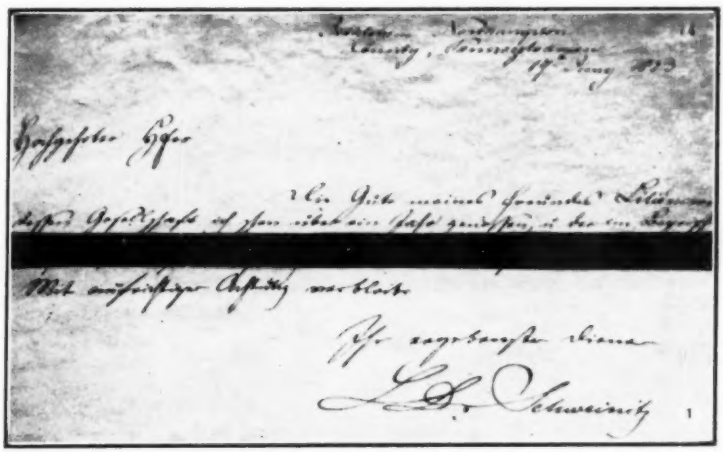

FIG. 1. Heading and conclusion of letter from Schweinitz to Fries.

jedoch noch 1200 auch europ. sind). Exemplare zuschicken, von den meisten welche preferable sind. Ihr Werk besitze ich bis ende die Fung. Clavat. und habe es nützlich gefunden. Seitdem ich mit Dr. Nees v. Esenbeck's und Ihrem System bekannt bin, habe ich dasselbe ganz angenommen und meine Fung. darauf rangiert. Wenn mir es die Zeit erlaubte könnte ich Ihnen viel interessante und für die Physiologie der Schwämme nicht unwichtiges aus meiner Beobachtung mitteilen, welche ich ein anderes Mal zu thun mir Erlaubnis erbitte, wenn es Ihnen angenehm ist. Ich habe Ihrer Sendung ein Verzeichniss das in meiner Sammlung (welche gegen 3000 Cryptogamisches enthielt) fehlenden Species beigelegt, nicht ohne Hoffnung dass Sie vielleicht Gelegenheit finden möchten

mir ein und anderes mitzutheilen. Sollten Sie die Gewogenheit haben mit mir eine correspondz zu wünschen so wollte ich bitten irgend etwas mir bestimmtes unter der Address Rev. L. D. de Schweinitz, Bethlehem N. County Pennsylvania durch den Schwedischen Consul in New York an mich gelangen zu lassen. Auch phaenogamische Seltenheiten wurden mir angenehm sein. Die Kürze meiner Zeit—da ich eben im Begriff bin mir weiter Reise in Amtsgeschäften nach Ohio anzutreten—zwingt mich abzubrechen und Sie nur zu bitten das Sie es mir gütigst verzeihen dass ich Ihnen vielleicht mit diesen Ansprüchen beschwerlicher falle, Ich schiebe alle Schuld auf meinen frd. Liliencron, der mich dazu ermuntert hat—und der Ihnen von meinen hiesigen Verhältnisse erforderlichen falls Auskunft geben wird. Mit aufrichtiger Achtung verbleibt

Ihr ergebenster Diener

L. D. v Schweinitz.

Bethlehem, Northhampton County,
Pennsylvania.
17th January 1823

My dear Sir:

My friend Liliencron, whose company I have enjoyed for over a year, is about to return to his homeland. Since he is so fortunate as to be one of your acquaintances, his kindness made it possible for me to write this letter, a pleasure I had anticipated for a long time. Your invaluable papers on mycology, a branch of science which is also my favorite, have my highest esteem, and I am taking the liberty of sending you a few hundred fungi of North America, hoping that this will please you. A considerable part of these fungi you will find mentioned in my little contribution which Dr. Schwägerichen had submitted for publication to the Leipzig Society. The others have been found since and as far as I know are only described in my unpublished papers. If agreeable to you, I could send the most desired of the 1600 species which I have found here and in my previous dwelling place in North Carolina. (However 1200 of these are also found in Europe.) I have your book to the end of the Fungi Clavat. and found it useful. After becoming familiar with the system of Dr. Nees von Esenbeck, a system which is also yours, I have accepted it fully and have classified my fungi accordingly. If time would permit, I could inform you of many interesting facts observed by me, and which are by no means unimportant for the physiology of the fungi. With your permission I shall do so at some other time. My shipment to you contains a list of all species which are missing in my collection (which has nearly 3000

Cryptogamicae), hoping that you might have time to let me have this or that. If you should be so kind as to wish to enter into correspondence with me, I would ask you to send anything designated to me under the address of Rev. L. D. de Schweinitz, Bethlehem, Northhampton County, Pennsylvania, care of the Swedish consul in New York. It would please me to receive also phanerogamic rareties. Lack of time—I am about ready to leave for a long official trip to Ohio—forces me to cut this letter short. Please pardon me kindly if my request should inconvenience you. I am putting the blame entirely on my friend Liliencron, who encouraged me to write you, and who will be able to give you all the information about the conditions under which I am living here.

With sincere respect I remain

Your most obedient servant,

L. D. v. Schweinitz

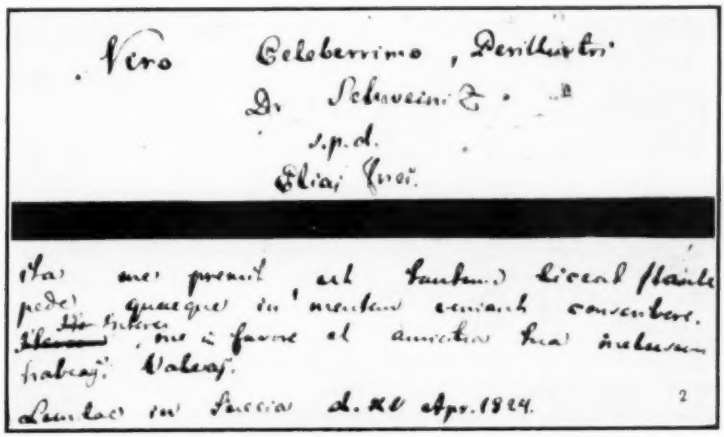

FIG. 2. Salutation and conclusion of Fries' reply to Schweinitz.

Viro celeberrimo, perillustri Dr. Schweinitz s. p. d. Elias Fries

Litteras suas humanissimas plantarumque collectionem ditissimam, cum amicissimo Liljecrona missam summa cum voluptate accepi, et quas gratias ago quantas possumo maximas. Quantum tibi debet mycologia certe meam superat laudem et quod illa collectione me cohonestaveris ex intimo pectore apto remunerare. Sed hodie unica modo hora concessa est, intra quam, quae tibi mittenda sunt, colligenda. Excusei igitur litteras has maxime interruptas, excusei plantarum exiguum numerum speciminaque

minus selecta. Certo certius mox transmittam amplam plantarum collectionem tam phanerogamarum, quam fungorum. Hac vice modo sequantur:

(1) Musci paucissimi.
(2) Lichenes rariores, desiderati 1 num.
(3) Scleromyc. Suec. Dec. I–XVIII, XIX–XXII, XXVII–XXX. Qui desidaruntur proxime mittam. Excusei, precor, quod hodie completa specimina mittere non valeo.

Plantas omnes americanas spontaneas, praecipue Lichenes et Phanerogamas, avidissimas desidero. Taceo fungos, non minus gratos. Observationes, quas communicare promiseris mihi certe perquam utiles erint. In Suppl. Syst. Myc. elaborando de loco Agaricorum Americanorum plurimorum dubius sum.

Secundum volumen Systematis Mycologici etiam grato amico hac vice exfero. Plures libros recentiores alia vice.

Finem imponam harum litterarum, quaram brevitatem et negligentiam iterum iterumque excusei precor. Summa temperi angustia ita me prevenit, ut tantum liceat stante pede quaeque in mentem veniant conscribere. Interea me in favore et amicitia tua inclusum habeas. Valeas.
Lundae in Suecia d. xv Apr. 1824.

To the most distinguished, most illustrious Dr. Schweinitz

Elias Fries sends most hearty greetings.

I have received with pleasure your very kind letter and the valuable collection of plants sent by the kindness of Liliencron, and express the greatest possible thanks for them. How much mycology owes to you is surely beyond my praise and I sincerely hope to return the favor of this collection with which you have honored me. But today I have only an hour in which to collect what is being sent to you. Therefore excuse this much interrupted letter, the small number of plants, and the poor selection of specimens. Very surely I will soon forward a large collection of plants, phanerogams as well as fungi. This time there are only the following:

(1) A very few mosses.
(2) More rare lichens, 1 number lacking.
(3) Scleromyc. Suec. Dec. I–XVIII, XIX–XXII, XXVII–XXX. The missing numbers I will send very soon. I beg you to excuse me for not being able to send the complete set today.

I am very eager to have any American wild plants, especially lichens and phanerogams. I do not speak of the fungi, which are no less welcome. The observations which you promise to communicate to me will certainly be exceedingly useful to me. I am

doubtful as to where to place very many of the American agarics in the Supplement to the Systema Mycologicum.

This time I am also sending to my valued friend the second volume of the Systema Mycologicum. Several more recent books at another time.

Let me close this letter, the brevity and carelessness of which I beg you again and again to excuse. The extreme shortness of time prevents me from being able to write at the moment what I have in mind. Meanwhile keep me in your favor and friendship. Farewell.

Lund, Sweden, Apr. 15, 1824

THE GENUS GOMPHIDIUS FRIES IN NORTH AMERICA

ROLF SINGER

(WITH 3 FIGURES)

DESCRIPTION OF GENUS

Pileus glabrous to tomentose or fibrillose, viscid or more rarely dry; hymenophore lamellate, consisting of rather thick, decidedly decurrent gills with frequently rather obtuse edges and waxy-gelatinous consistency; lamellae moderately close, subclose to distant, arcuate, later descendant, gray to fuliginous when mature; spore print between "bone brown" and black, usually fading out to deep rusty brown in old spore prints; spores melleous to gray, fusoid to ellipsoid-cylindric, smooth, with thin to slightly thickened but simple non-amyloid walls and without a germ pore; sterigmata usually with a very broad base, mostly four on a basidium; basidia voluminous and variable in length; cystidia present on the edges and on the sides of the lamellae, often appearing more scattered in old specimens because of the collapsing of the walls, sometimes slightly colored but more often hyaline except for a colored resinous incrustation, large, thick- or thin-walled, originating in the subhymenium; trama thick, consisting of an often rudimentary mediostratum, a lateral stratum of non-divergent hyphae, and an irregular hymenopodium which is rather indistinctly limited from a filamentous-intermixed or filamentous to filamentous-cellular subhymenium; hyphae without clamp connections; stipe frequently with a yellow lower portion; context thick in the middle of the pileus and at least in some parts of it (especially under the cuticle) strongly reacting with most of the usual inorganic reagents; veil present, cortinoid or glutinous-hyaline, rarely glutinous and fugacious at an early stage; mycelium white or colored, forming mycorrhiza with conifers. This genus has its natural affinities with the Boletineae.

Type species: *Gomphidius glutinosus* (Schaeffer ex Fr.) Fr.

KEY TO SUBGENERA AND SECTIONS

A. Context of the pileus ochraceous to orange (though at times in young specimens rather pallid), more rarely salmon to pink; veil constantly present, consisting of strictly parallel, pigment-incrusted hyphae, macroscopically never entirely glutinous, never hyaline; subhymenium filamentous-intermixed and dense to very dense; mediostratum rudimentary in young specimens, indiscernible in adult ones..Subgenus I. CHROOGOMPHUS
  B. Pileus dry to subviscid in wet weather, not shining in dry weather, more or less tomentose to fibrillose .....Section *Floccigomphus*
  B. Pileus viscid in wet weather, shining in dry weather, not tomentose and not fibrillose except for traces of the veil on the margin. Section *Viscogomphus*

A. Context of the pileus white, more rarely partly more or less salmon, or becoming so on exposure; veil absent, or consisting of subparallel-subinterwoven, thin hyphae which are not incrusted by pigment, microscopically hyaline to white, and often partly or entirely glutinous, sometimes gradually blackening in age; subhymenium filamentous-cellular to filamentous, moderately dense; mediostratum of young specimens distinct, less distinct in older ones.
  B. Veil visible only in the primordium, fugacious and not leaving any traces in adult specimens; dermatocystidia of the stipe fasciculate and the fascicles forming glandulae which make the stipe appear fibrillose or furfuraceous (though these macroscopical characters not always very obvious); mycelium (of *G. maculatus*) connected with *Larix*-mycorrhiza .....Subgenus II. LARICOGOMPHUS
  B. Veil covering the lamellae of young specimens and leaving more or less distinct traces even in old specimens; dermatocystidia of the stipe not fasciculate; no fibrils or glandulae made up of dermatocystidia present on the surface of the stipe; mycelium in nature not connected with larch but rather forming mycorrhiza with a variety of other conifers (*Pinus, Picea, Tsuga, Pseudotsuga, Abies*). Subgenus III. MYXOGOMPHUS
    C. Spores (with exception of immature and aborted ones) longer than 14 μ .....Section *Macrosporus*
    C. Spores, or majority of spores, of a mature carpophore, shorter than 14 μ, or just reaching 14 μ .....Section *Microsporus*

SUBGENUS CHROOGOMPHUS Singer

Papers Michigan Academy Science Arts and Letters **32**: 150. 1948

Section *Floccigomphus* Imai

Journ. Agr. Hokk. Imp. Univ. **43**: 285. 1938

KEY TO SPECIES

A. Cystidia thick-walled (walls 1–4 μ thick), never collapsing, numerous in old specimens .....1. *G. tomentosus*
A. Cystidia thin-walled (walls up to 1 μ thick), collapsing in poorly dried or very old material and then not readily demonstrated ..2. *G. leptocystis*

1. GOMPHIDIUS TOMENTOSUS Murrill
Mycologia **4**: 307. 1912

Pileus fleshy, thick, abruptly thin at the incurved margin, ovoid-subhemispheric to convex when young, later convex and expanding, in age often plane and with uplifted margin, the disc often conical at first, later often umbonate, more rarely umbilicate or depressed around a papilla, 20–100 mm. broad, surface innately and appressedly tomentose, moist to somewhat sticky-subviscid in very damp weather, not becoming scaly except in age and then because of the breaking up of the surface layer or because of the disintegrating of the tomentum into tomentose, strictly appressed squamulae, disc sometimes rugulose or uneven, margin fringed at first with the fibrillose remnants of the veil, uniformly "ochraceous buff," or "capucin buff," or "pale yellow orange," or "light ochraceous salmon," or "light ochraceous buff," or "pinkish buff" (the color depending on the amount of moisture present, *e.g.*, "pinkish buff" appearing with low moisture content, etc.), the fibrils sometimes assuming a slight pinkish-vinaceous tinge, especially in age when the disc tends to become "zinc orange"; flesh about "ochraceous orange" or "capucin buff," or "ochraceous buff," or cortex near "capucin orange," unchanging, with KOH and NH_4OH purple, with $FeSO_4$ entirely olivaceous gray, with formol negative, soft and rather pliant when fresh, odor slight, agreeable, or none, taste slight, tardily slightly disagreeable; lamellae decurrent, inserted, subclose to distant, a few forked, broad but narrow in small specimens (3.5–12 mm.), often wrinkled or venose near the margin, concolorous with the pileus, then sooty from the spores; spore print about "bone brown" to nearly black; spores (16.5) 17–24.5 × 6.5–9 μ, most frequently 18.5–20.2 × 7.5–8.2 μ, ellipsoid, pale sordid-melleous, some deeper colored, comparatively broad; basidia 40–56 × 11–13.5 μ, 4-spored; cystidia 136–242 × 14–24 μ, ventricose, capitate, or cylindric, sometimes with narrowed apex which, however, is always rounded, the walls thick (1–4 μ) but in a few cystidia sometimes thin, their outer surface often incrusted by a fulvous-castaneous to melleous resinous incrustation, their inner surface also sometimes colored or the lumen filled with a colored sap, numerous on both the sides and edges of the lamellae and never collapsing; subhymenium filamentous-intermixed, dense; trama with a slight mediostratum which soon becomes indefinite; lateral stratum with a distinct axillar arrangement of subparallel-subinterwoven hyphae, looser than the hymenopodium which is scarcely delimited from the subhymenium, often with pink areas in freshly dried material; stipe subequal or tapering gradually or abruptly at the base, or

subventricose, solid, fibrillose or loosely tomentose to innately flocculose with scurfy apex, glabrescent, "light orange yellow" (from the veil), or concolorous with pileus, "ochraceous orange" when scratched, 40–100(180) × 5–20 mm.; context concolorous with the context of the pileus, the periphery concolorous with the scratched surface, neither bright yellow nor deep orange in the base, unchanging, rather soft, usually turning pinkish in well dried specimens; mycelium pink, the basal tomentum consisting of thin- or thick-walled hyphae 8–17 μ in diam., occasionally incrusted by a melleous or hyaline incrustation, interwoven, cylindric, and all hyphae without clamp connections.

Type locality: Seattle, Wash., New York Botanical Garden (type seen).

Habitat: Among mosses or on naked clay-soil in coniferous woods near *Pinus, Abies, Tsuga, Pseudotsuga,* etc., scattered to very gregarious up to the subalpine zone, fruiting from September to November.

Distribution: Washington to California (gradually becoming more uncommon toward the south), also in Hokkaido and Honshu, Japan.

Note: A. H. Smith has collected a subalpine form with stouter stipes (30–60 × 10–30 mm.) but otherwise identical with the type form. *G. tomentosus* sensu Kauffm. is *G. tomentosus* Murr. plus *G. leptocystis. G. tomentosus* sensu Humbolt is *Cystogomphus Humboltii* Sing.

2. GOMPHIDIUS LEPTOCYSTIS Singer (Figs. 1–2)

Papers Michigan Academy Science Arts and Letters **32**: 148. 1948

Pileus fleshy, thick, abruptly thin at margin, campanulate, ovalhemispheric, soon expanding, convex then plane, or somewhat depressed, obtuse or more rarely with an acute or obtuse umbo, 30–90 mm. broad, surface strongly felty-fibrillose when young, later the felt breaking up to form hairy scales on the disc and around it where the dried pileus assumes a squarrulose appearance, less so on margin, the hairs "ochraceous buff" on "buckthorn brown" ground, sticky-subviscid and "vinaceous tawny" to "wood brown," or "drab" near the margin and more yellowish toward the disc in very damp weather, "ochraceous orange" to "ochraceous buff" in dry weather, tending to assume a "deep brownish vinaceous" ground color and darker (to "warm blackish brown") spots and fibrils giving the general impression of about "Prussian red," "deep

livid brown," "Mars violet" where wounded or when freshly dried; this purple color due to a purple incrustation of the hyphae which turns melleous in KOH; the pellicle separable from the context which is paler, nearly whitish, and shot through with streaks of "pinkish buff" or slightly changing to purplish in places, inodorous, taste tardily and slightly disagreeable; lamellae usually unequally

Photo A. H. Smith.

FIG. 1. *Gomphidius leptocystis.* × 1.

decurrent, inserted, close to subdistant, a few forked, often anastomosing, with entire edges, broad (6–13 mm.), "ochraceous buff" to "ochraceous salmon," at last "clay color," "ochraceous tawny," sooty from the spores; spore print nearly black; spores 14–20 × 6–8.2 μ, mostly about 16–17 × 6.8–7.3 μ, ellipsoid to fusoid, pale sordid melleous, some deeper colored; basidia 38–68 × 11–13 μ, 4-spored; cystidia 120–238 × 12–21 μ, hyaline with a ful-

vous-castaneous resinous incrustation, or with a melleous granular incrustation, with thin (up to 1 μ) walls or very few occasionally up to 1.5 μ thick, the inside of the walls not colored (except in very few cystidia in occasional specimens), easily collapsing by careless preparation, in age readily collapsing and hence appearing scattered in old specimens; all hymenial bodies and even the hyphae initially with a

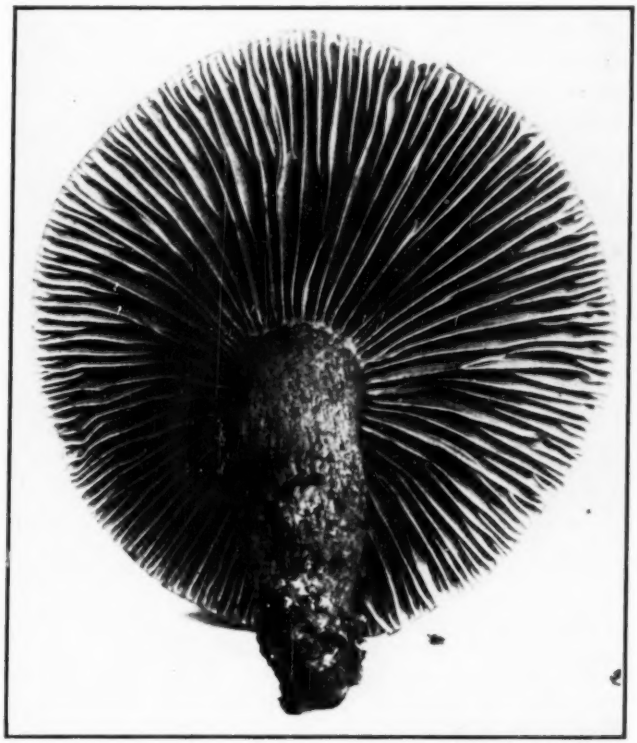

Photo A. H. Smith.

FIG. 2. *Gomphidius leptocystis.*

purple incrustation (NH_4OH) when freshly dried, the incrustation becoming melleous in alkali; trama and subhymenium as in *G. tomentosus;* stipe subcylindric or attenuated below, sometimes fusiform, mostly rather long, occasionally short, fleshy solid or hollowed by grubs in age, floccose then lacerate-floccose, the floccosity initially continuous with that of the pileus, the lower portion often denudate by being deeply imbedded, apex with slight remnant

of the fibrillose-silky "buff yellow" to "maize yellow" veil, otherwise colored as the pileus and becoming purplish by handling and drying, downward becoming "empire yellow" or sordid ocher-brown, 60–130 × 8–25 mm.; context in the upper portion concolorous with that in the pileus, in the base "empire yellow," rather hard and rigid; mycelium pinkish; all hyphae without clamp connections.

Type locality: Lower Stony Creek, Garibaldi, B.C. J. E. Davidson *222* (type at Michigan University Herbarium).

Habitat: Mostly in deep needle beds and on humus, in mixed coniferous woods under or near pines, scattered to gregarious, fruiting from August to October.

Distribution: Northwestern part of North America: British Columbia to Oregon and East to Idaho.

Illustration: Kauffman, Mycologia **17**, pl. 14. 1925 (as *G. tomentosus*).

Note: This species differs from *G. tomentosus* in the characters of the covering of the pileus, in the pigment, in the thin walls of the cystidia, and in somewhat smaller average spore size. It differs from the closely related *G. sibiricus* in the color of the base of the stipe which is "empire yellow" instead of deep orange.

Section *Viscogomphus* Imai
Journ. Fac. Agr. Hokk. Imp. Univ. **43**: 284. 1938

KEY TO SPECIES

A. Mycelium pink or pallid-salmoneous.
  B. Cystidia thick-walled in their middle portion .....3. *G. vinicolor*
  B. Cystidia thin-walled throughout .....4. *G. ochraceus*
A. Mycelium Isabella color, or melleous, or light to bright yellow; cystidia thin-walled throughout .....5. *G. rutilus*

3. GOMPHIDIUS VINICOLOR Peck
N. Y. State Mus. Rep. **51**: 291. 1898

Pileus usually thick and fleshy at least in the center, thinning out toward the margin, conic-convex, then convex, usually umbonate, or at least the majority of the pilei of a group umbonate, 10–90 mm. broad; surface viscid, shining when dry, glabrous, naked, smooth, rarely diffracted in age, ochraceous gray or between "Army brown" and "Natal brown," becoming deep reddish brown ("Mikado brown," "chestnut," "liver brown," "carob brown"), eventually of-

ten deep vinaceous red; pellicle consisting of repent, subparallel-subinterwoven, fulvous-castaneous-incrusted, elongate hyphae; context pale ochraceous to "pale ochraceous salmon," sometimes very slightly turning pinkish on injury, sometimes umber immediately beneath the pellicle, with KOH between "pale rosolan purple" and "thuilite pink," and becoming "spinel red," with NH_3 vapors "liseran purple" and "pale rosolan purple," with $FeSO_4$ "deep olive" to "dark olive" or more olive gray; with formol negative; lamellae initially dirty ochraceous-alutaceous, becoming between "Prout's brown" and "mummy brown," eventually almost black from the spores, broadest in the middle (4–9 mm., *i.e.*, broad), decurrent, arcuate, or arcuate-plane, inserted, slightly transversely venose, or smooth, only rarely and very sparsely forked, subdistant to distant; spore print from "clove brown" or "olive brown" to nearly black; spores (17) 18.5–26 × 6–7.5 μ, melleous-pallid to melleous grayish, or melleous, ellipsoid to cylindric or fusoid; basidia 45–61 × 12–15.7 μ, 4-spored; cystidia 108–177 × 13.6–19 μ, numerous though not unusually crowded, on the edges as well as on the sides of the lamellae, strongly incrusted on the outside by a castaneous-fulvous resinous mass, and slightly incrusted in some cases on the inside of the walls which are thin to moderately thick at the apex and thin at the very base but distinctly thickened (1.3–5.8 μ) either in the middle or just below the middle, hyaline, cylindric or slightly ventricose below; subhymenium filamentous-intermixed, very dense and irregular; mediostratum of very few, parallel, cylindric hyphae, indistinct or soon disappearing; lateral stratum less dense and more hyaline, subirregular with an axillar arrangement but becoming more and more irregularly interwoven with age; hymenopodium only slightly distinct from the subhymenium, strongly colored; stipe subequal or gradually tapering downward, not viscid, glabrous except for the veil, smooth but sometimes grooved when drying, naked, sordid ochraceous to "light vinaceous cinnamon" to "buff pink," or "vinaceous rufous," the base mostly "cinnamon" to "clay color," "light ochraceous buff" or "ochraceous buff," sometimes at places becoming "orange rufous" to almost "Jasper red" or "orange cinnamon" or "cacao brown," sometimes with blackish spots on handling, solid, 27–95 × 3–14 mm.; veil either forming a definite fibrillose-woolly narrow annulus which is concolorous with the remaining surface, or reduced to a mere fibrillose zone at the apex of the stipe and consisting of strands of parallel, incrusted hyphae; mycelium pinkish; context similar in color to that of the pileus but either more "clay color" or more "primuline yellow" at the base in many specimens; odor none or very slight, agreeable; taste mild; the context of the base turning olive with NH_3, brownish with NH_4OH, deep fulvous-yellow with H_2SO_4 (if dried subsequently),

olive as in the pileus with $FeSO_4$; all hyphae without clamp connections.

Type locality: Lake Mahonk, N. Y., U. S. A. (New York State Museum, type seen).

Habitat: Under *Pinus Murrayana, P. resinosa, P. rigida, P. virginiana,* or near one of these species in mixed woods, on the ground, gregarious, fruiting from August to November.

Distribution: From Maine to Tennessee and from Ontario across the continent to British Columbia, Washington, Oregon and the mountainous part of Northern California.

Note: This is considered as ssp. *typicus* of the species. Peck's types are this. It is the northern race of the complex species consisting of geographic and ecologic races. It differs from ssp. *jamaicensis* in slightly more distant lamellae, slightly larger spores, and the presence, in most specimens, of an umbo; it differs from ssp. *californicus* in the smaller number of cystidia present, and also in the presence of an umbo and more distant lamellae; all these races differ in their geographic areas and the pine species with which they form mycorrhiza in nature.

Ssp. JAMAICENSIS (Murr.) Sing., Farlowia **2**: 531. 1946

Gomphidius jamaicensis Murr., Mycologia **10**: 69. 1918.
Gomphidius alachuanus Murr., Journ. Elisha Mitch. Soc. **55**: 367. 1939.

Pileus consistently exumbonate in mature specimens, never red, 24–98 mm. broad; lamellae subclose to subdistant; spores 17–21.8 × 5.8–8 μ, melleous grayish to gray; basidia 34–46 × (8.3) 9.2–13 μ; 4-spored; cystidia 115–150 × 13.5–22.5 μ, thick-walled in the middle; stipe 36–100 × 4–15 mm., rarely becoming black on handling; all other characters practically identical with those of the type subspecies. Habitat: Under *Pinus taeda,* and probably also under *P. caribaea, P. australis,* and *P. palustris,* on the ground in sandy woods, or near these pines in mixed woods, gregarious, fruiting from November to January; North Florida and Alabama, also in the Mountains of Jamaica.

Ssp. CALIFORNICUS Singer, Pap. Mich. Acad. **32**: 149. 1948

Pileus obtuse or subumbonate, more rarely distinctly umbonate, usually rather large to very large; lamellae subclose to subdistant;

cystidia extremely crowded and almost as numerous as the basidia; all other characters including the spore size exactly as in the typical form. Under or near *Pinus radiata* and *P. ponderosa* on soil preferably rich in nitrogen, often subcespitose, from late fall until spring in California.

4. GOMPHIDIUS OCHRACEOUS Kauffman ssp. TYPICUS Mycologia **17**: 119. 1925

Pileus fleshy, abruptly thin at the margin which is at first incurved, convex, then becoming plane, often with decurved margin and the disk slightly depressed around the umbo, but just as often without any umbo or with a very indistinct one, 15–75 mm. broad; surface viscid, shining when dry, glabrous, smooth or sometimes rugulose from the drying gluten, "ochraceous salmon," "apricot orange," "deep chrome" on the margin when fresh, "zinc orange" to "ochraceous orange" elsewhere but sooner or later more or less clouded with "olive brown" or grayish in the center, then also near the margin and gradually becoming some tint around "vinaceous tawny" or plainly vinaceous, "Indian red" to "dark Indian red" in recently dried specimens; pellicle thick and toughish, separable; context whitish with a tinge of "pinkish buff" to evenly "light ochraceous buff," with KOH and NH_4OH pinkish to purple, with $FeSO_4$ greenish-gray and finally inky-violaceous, with formol negative, odor none, taste mild; lamellae decurrent, close to distant, inserted, rather broad (about 7–8 mm. in larger caps), "tawny" or ochraceous, soon sooty from the spores; spores 17–20.5 (22) × 6.5–7.3 (8) μ, fusoid-ellipsoid, pale sordid melleous, some deeper colored; basidia 47–56 × 11–15 μ, 4-spored; cystidia 116–185 × 11–16.5 μ, very numerous on edge and sides, cylindric or ventricose, thin-walled (walls up to 1 μ thick not counting the incrustation), hyaline with strong hippocastanus-brown resinous incrustation; subhymenium, hymenopodium, lateral stratum and mediostratum as in *G. leptocystis;* stipe tapering downward, slightly curved or flexuous, more rarely straight, "orange buff," or concolorous with some part of the pileus, at last partly vinaceous, flocculose-fibrillose to an obsolete cortinoid annulus and this fibrillosity with a strong tendency to become subviscid to viscid on its outer side in a humid atmosphere but soon drying out in drier weather, 30–185 × 4–20 mm., veil concolorous with the rest of the stipe, consisting of parallel hyphae which are strongly incrusted by pigment; context concolorous with the surface; mycelium pink; all hypae without clamp connections.

Type locality: Mt. Hood, Ore., University of Michigan Herbarium (type seen).

Habitat: Under conifers (*Pinus monticola, Abies* spec., *Pseudotsuga, Tsuga,* probably usually connected with *Pinus monticola*), mostly gregarious, fruiting from September until later in fall.

Distribution: From Washington to Northern California.

Note: The above description is given for the Western race with the yellow-ochraceous-orange margin of the pileus and somewhat orange stipe. It is not only the nomenclatorial type but probably also the form most closely related to the one from which all American subspecies originated, and on the other hand, more closely related to the species of the preceding section than any other species or race in this section.

Ssp. **muscigenus** Singer * ssp. nov.

Pileus moderately fleshy, constantly with a small acute umbo, 15–50 mm. broad; surface "bay" or "auburn," or "tawny," or "Hay's russet," or between "buffy brown" and "olive brown," with the margin often more yellowish brown (*e.g.,* "ochraceous tawny" or more dingy then "salmon buff"); lamellae macroscopically and anatomically as well as the spores not different from the type of *G. ochraceous;* stipe "ochraceous orange," mixed with "ochraceous tawny" and "light buff," or "capucin buff" to "capucin orange," becoming "apricot orange" or "light salmon orange," 35–80 × 4–10 mm.; mycelium "flesh pink"; context concolorous with the surface or more yellow below ("Naples yellow," slightly tending toward "warm buff" and "massicot yellow") but between "pale pinkish buff" and "pinkish buff" at the very base; otherwise like ssp. *typicus.* Under or near pines of the subgenus *Haploxylon,* very often in sphagnum-swamps or otherwise in deep moss beds, but also in deep needle beds and on very decayed wood; from Maine and Ontario to New York and West to Wyoming; Icon. Farlow. pl. 70 (*G. viscidus* var. *testaceus*); usually associated with *Suillus americanus.*

Ssp. **superiorensis** (Kauffm. & Smith) Singer comb. nov.

G. superiorensis Kauffman & Smith, Pap. Mich. Acad. Sci. **17**: 170. 1933.

Pileus "Natal brown," "army brown," also "pecan brown"; stipe and cortina "ochraceous buff," otherwise like ssp. *muscigenus.*

* A typo colore pilei haud ochraceo-aurantiaco et probabiliter associatione mycorhizina differt.

Under *Pinus resinosa* and possibly other pines of the subgenus *Diploxylon* in sphagnose places in Michigan. Illustration: Kauffman & Smith, Papers Mich. Acad. Sci. 17, pl. 30.

5. GOMPHIDIUS RUTILUS (Schaeff. ex Fr.) Lundell & Nannfeldt Fungi Exsicc. Suec. 409. 1937

Agaricus rutilus Schaeff. ex Fr., Syst. Myco. **1**: 315. 1821.
Cortinaria rutila S. F. Gray, Nat. Arr. Brit. Pl. **2**: 629. 1821.
Gomphidius viscidus (L. ex) Fr., Epicr. p. 319. 1838.
Gomphidius testaceus (Fr.) Britz., Hymen. Sudb. **4**: 133. 1885 (a var.).
Gomphidius litigiosus Britz., Hymen. Sudb. **9**: 14. 1893 (a var.).
Gomphidius alabamensis Earle (Nom. subnud.) (ssp. *alabamensis* Sing.).
Gomphidius viscidus var. *columbiana* Kauffm., Mycologia **17**: 122. 1925.

Pileus conic to campanulate with incurved margin, then expanding, with umbo or rarely without umbo, the margin often eventually uplifted, 15–60 mm. broad; surface with a fibrillose "apricot buff" veil-zone on young caps, otherwise glabrous, smooth but frequently cracking in age and becoming scaly, viscid except on the veil-zone, soon entirely viscid in wet weather but not glutinous, usually "olive brown" when quite young, later with yellow tints, becoming "vinaceous tawny" to "Rood's brown" or "Hay's russet" when old, at last sometimes reaching "light russet vinaceous" or even "Indian red," with H_2SO_4 pale brown (almost no reaction); context pale brownish buff, or more reddish, sometimes sordid-pallid, with KOH lilac, with NH_3 violet then violet blue, with $FeSO_4$ olive-gray to deep greenish black; odor none or slight, fruity; lamellae "ochraceous tawny" or paler when young, then "vinaceous brown," "Prout's brown," "Saccardo's umber," "tawny olive," or "sepia," subdistant to distant, simple or very few forked, broad (5–8 mm.), inserted, decurrent; spore print between "clove brown" and black; spores (15) 18.5–23 × (5) 6–7.8 μ, ellipsoid-elongate to subfusoid, or subcylindric, sordid-melleous; basidia 40–54 × 14–15 μ, 4-spored; cystidia 60–170 × 12–21 μ, numerous on edges and sides of the lamellae, thin-walled throughout, subcylindrical, ventricose or capitate, with a strong resinous incrustation of mahogany-brown to hippocastaneous-brown, more rarely honey color; subhymenium filamentous-intermixed and very dense, appearing irregularly cellular when looked upon superficially, colored; mediostratum axillar, of loose, parallel hyphae, indistinct from the beginning and soon entirely obliterated; lateral stratum non-divergent, of subparallel-interwoven hyphae, looser than the hymenopodium which is not much different from the subhymenium

but having mostly somewhat larger elements than the latter; stipe "ochraceous buff," pallid at the very apex, at least initially, but soon concolorous or "Buckthorn brown," or covered with colored fibrils or with the spores, fibrillose from the veil which gives it a "flesh ocher" to "apricot orange" color, or becoming pinkish red with age, dry and equal or tapering downward, solid, often becoming somewhat hollow from grubs, often slightly compressed or wavy and flexuous, 30–80 × 6–15 mm.; mycelium "honey yellow," "Isabella color," or "Naples yellow," "mustard yellow," "primulin yellow," or mixtures of these and white; context of the stipe concolorous with the flesh of the pileus in the upper portion, *i.e.*, a pale yellowish buff, often becoming "apricot orange," richer yellow toward the base; all hyphae without clamp connections.

Type locality: Regensburg, Bavaria (type specimens not preserved).

Habitat: On bare soil and among needles, also among mosses but usually not in sphagnetum, accompanying pines of the subgenus *Diploxylon*, in this Hemisphere excusively with pines of the series Insignes (*e.g.*, *Pinus Murrayana, P. radiata*), fruiting from summer until late fall, or spring (in California).

Distribution: From the Rocky Mountains to the Pacific Coast, also in Europe and Northern Africa, Northern Asia, east to Hokkaido and Honshu, Japan.

Illustrations: Represented in almost all European mushroom books and illustrated scientific manuals, best in Lange, Flora Agar. Dan. 5; Kavina, Ceske Slizaky, Trav. Mycol. Tchecosl. 2, fig. 8, etc. (see Saccardo, Syll. **19**: 789 sub *Gomphidius viscidus*).

Exsiccata: Saccardo, Mycotheca Veneta 810; Roumeguere, Fungi Gallici 3815; Fuckel, Fungi Rhenani 1429.

Note: The above described form includes the American plant which Kauffman distinguished under the name var. *columbiana*. The European form grows with pines of the series Lariciones while the American form is found near pines of the series Insignes. Except for this physio-ecological difference, which by the way escaped Kauffman because he had no clear conception of his variety, we are unable to confirm any of the minor differences enumerated and discussed by Kauffman. The type of var. *columbiana* is identical with the European *G. rutilus* of which we distinguish only a ssp. *typicus* as described above, with var. *typicus*, var. *testaceus*, and

other varieties of European importance only, and ssp. *alabamensis* occurring in the Southern States of this country:

Ssp. ALABAMENSIS Earle ex Singer, Farlowia **2**: 535. 1946

This differs from the type subspecies in the absence of an umbo (at least in the vast majority of mature specimens), the more furfuraceous than fibrillose apex of the stipe, and the more frequently bright yellow base of the stipe, and perhaps some minor characters of doubtful constancy. It grows near pines of the series Australes and Insignes from Maryland to Northern Florida, and west to Tennessee and Alabama. The type was collected by Earle in Alabama but is here considered as a nomen subnudum, published in a key to the species of *Gomphidius* but never described properly.

SUBGENUS LARICOGOMPHUS Singer
Papers Mich. Acad. Sci. Arts and Letters **32**: 149. 1948

KEY TO SPECIES

A. Pileus "vinaceous pink" when young; spores 23.5–32 × 7.5–8.2 μ. ..... 7. *G. flavipes*

A. Pileus more brownish than "vinaceous pink," or whitish when young; spores 18–25 × 7–9 μ ..... 6. *G. maculatus*

6. GOMPHIDIUS MACULATUS (Scop. ex Fr.) Fries
Epicr. Syst. Myc. p. 319. 1838

Agaricus maculatus Scop. ex Fr., Syst. Myco. **1**: 315. 1821.
Cortinaria viscida atropuncta Gray, Nat. Arr. Brit. Pl. **2**: 629. 1821.
Gomphidius gracilis Berk. & Br. apud Berk., Outl. Brit. Fungology, p. 196. 1860.
Gomphidius maculatus var. *gracilis* Quél., Enchir., p. 91. 1886.
Gomphidius furcatus Peck, Bull. N. Y. State Mus. **5**: 649. 1899 (a variety).
Gomphidius maculatus f. *gracilis* Kavina, Trav. Mycol. Tchec. **2**: 5. 1924.
Gomphidius maculatus ssp. *gracilis* Konr. & Maubl., Icon. Sel. Fung. **4**: pl. 329, **6**: 442. 1924–1938.
?*Gomphidius stillatus* Strauss in Sturm, Deutschl. Flor. III, **33–34**: 3. 1853 (see also "Doubtful species").

Pileus convex, eventually plane or irregularly depressed, umbonate or obtuse, 20–110 mm., surface viscid to glutinous, glabrous and smooth, rarely with some slight pallid fibrils in young specimens, dull fuscous pink to reddish brown in varying intensity, most

frequently "light pinkish cinnamon" to "orange cinnamon," but sometimes almost pallid or whitish and often later assuming a reddish tone because of the reddening of the underlying context, reaching "dragon's blood red" or "Hay's russet," usually becoming stained with black more readily than other species; hyphae of the cuticle incrusted, 4–14 μ thick, a few terminal members cystidium-like and obtusely rounded at the ends, olive colored in NH_4OH; context white, lemon yellow toward the base, when injured reddening in the white portion to pink, latericious, or almost wine red, but the reddening often failing to develop in dry weather or in too watery material, with a watery, then brick red line just beneath the cuticle; odor none, or of cumarin; taste mild; context becoming dark green with $FeSO_4$, intensely brick color with NH_3 and NH_4OH; with formol lilac-red; lamellae short decurrent to decidedly decurrent, usually many-forked, subdistant to distant, variable in breadth, pallid, then gray, often somewhat reddening; spore print black or nearly so; spores 18–25 × (6) 7–9 μ, dark brownish gray, some paler, subfusoid; basidia 38–66 × 10–17 μ, 4-spored; cystidia (100) 133–216 × 16–26.5 μ, numerous, fusoid, rounded above, the apex attenuate or cylindrical, mostly filled with a gray sap, covered with grayish brown to dark gray incrustations, strongly (80–100 μ) projecting, thin-walled; subhymenium filamentous or filamentous-subcellular, rather loose, mediostratum moderately distinct in very young specimens, later becoming rather indistinct; stipe immensely variable in shape, pallid whitish, or reddish pallid, intensely yellow to lemon yellow at the base, mostly covered with reddish bay glandulae which sooner or later become blackish, tending to blacken partly or entirely by pressure or on drying, beset with colorless watery droplets at the apex in many specimens, the droplets becoming brownish or reddish after a short time, but in dry weather the glandulae often inconspicuous and covering only a narrow zone of the stipe, solid, 40–80 × 3–35 mm.; glandulae consisting of fascicles of dermatocystidia, dermatocystidia olive black in NH_4OH, little or not incrusted, about 100 μ long and 8–13.5 μ thick, cylindric; context concolorous with the surface and otherwise as in the pileus; mycelium whitish to yellowish; all hyphae without clamp connections.

Type locality: Carniola (type not preserved).

Habitat: In larch woods and tamarack swamps (in America mostly near *Larix laricina* = *L. americana*), associated with Suilli of the section Larigni (*S. aeruginascens, S. Grevillei* var. *Clintonianus* and others), fruiting from July to October.

Distribution: From New England to North Carolina and west to Michigan and Ontario, possibly also farther west and north, but infrequent at most localities; also in Europe and Asia (as far as the area of *Larix* extends).

Illustrations: Kauffman, Agar. Mich. 2, pl. 23; Cooke, Illustr. pl. 883; Lucand, Champ. Fr. pl. 346 A–B; Ricken, Blätterp. 2, pl. 3, fig. 2; Bresadola, Icon. Myc. 14, pl. 675. The remaining figures are rather poor: Berkeley, Outl. pl. 12, fig. 7; Britzelmayr, Hym. Sudb., Gomph. fig. 9, 11, 12; Cooke, Illustr. pl. 882; Bresadola, Iconogr. 14, pl. 674; Konrad & Maublac, Icon. 4, pl. 389.

Note: Eurasiatic specimens more often have broader than narrower spores, while in the American specimens this situation is reversed.

Var. **furcatus** (Peck) Sing. comb. nov. (*G. furcatus* Peck, l.c.). Base of the stipe not bright yellow. Type from Kasoag, N. Y., distribution unknown.

7. GOMPHIDIUS FLAVIPES Peck

N. Y. State Mus. Rep. **54**: 153. 1901

Pileus convex, expanded and repand in age, obtuse or subumbonate, 15–40 mm. broad; surface even, viscid, the viscidity soon slight, with a thin, minutely tomentose (?) pellicle with silky fibrils on the margin, "vinaceous pink" when fresh, becoming duller in age; lamellae arcuate, subdecurrent, distant, very few forked, thick, "pale pinkish buff," at last sprinkled by the spores, 4–5 mm. broad midway between margin and stipe, often transversely wrinkled, edge entire; spores (20.5) 22.5–32.5 × (6) 7–8.2 μ, fusiform, more rarely clavate, fuscous; basidia 48–58 × 11.2–15 μ, 4-spored, very few 2-spored; sterigmata 8–10.5 μ long; cystidia 90–136 × (10) 15–20.5 μ, numerous, subcylindric or slightly ventricose, broadly rounded at the apex, hyaline; subhymenial and tramal characters as in *G. maculatus;* stipe equal above, tapering below to a pointed base, silky or lacerate-silky at apex, slightly fibrillose downward, white above, "picric yellow" or bright below (the yellow often reaching to the apex) both inside and out, solid becoming soft, sometimes curved or twisted, 50–80 mm. long; fibrils of the upper portion of the stipe consisting of fascicles of dermatocystidia which are either of the same shape as the hymenial cystidia, or more clavate, ventricose, etc., mostly hyaline; odor none; taste mild (macroscopical characters from Kauffman & Smith).

Type locality: Westport, N. Y., State Museum (type seen).

Habitat: In sphagnose bogs (the accompanying conifers unknown), fruiting from August to September.

Distribution: From New York to Michigan.

Illustrations: Peck, l.c., pl. I, fig. 1–4.

Note: This rare species may be a variety of *G. maculatus* but its glandular fibrils do not blacken and its dermatocystidia are hyaline, its spores are notably longer (the longest in the genus), and the color of the fresh pileus is more pink. The species has been placed in *Laricogomphus* tentatively, without regard to the lack of information on the tree symbiont and the reactions of the context.

SUBGENUS MYXOGOMPHUS Singer

Papers Mich. Acad. Sci. Arts and Letters **32**: 149. 1948

Section *Macrosporus* Singer

Papers Mich. Acad. Sci. Arts and Letters **32**: 149. 1948

KEY TO SPECIES

A. Veil essentially fibrillose, or partly fibrillose and partly glutinous, in the latter case the glutinous portion manifesting itself in the mature specimen by forming 1–3 slimy belts at the apex of the stipe but never forming a wide glutinous sheath; context salmon color in fresh and dried specimens, except for the lower portion of the stipe which is deep brilliant yellow .....8. *G. septentrionalis*

A. Veil essentially glutinous, or merely the inner layer fibrillose, the glutinous portion forming a conspicuous slimy sheath that covers most of the surface of the stipe and terminates, toward the apex, in a glutinous annular thickening of the slime layer, or in a crown of very fine, very narrowly distant silky fibrils which gelatinize in prolonged wet weather; context white or partly becoming slightly pinkish in age, or turning pinkish on injury, especially in the upper (subhypodermial) zone; base of the stipe either white or yellow.

B. Eastern species with concolorous (white) base, associated with white pine (*Pinus strobus*); a substantial percentage of the cystidia and subhymenium in most specimens strongly colored gray; pileus at first whitish, then pink; pileus and stipe usually rather small and thin.
9. *G. nigricans*

B. Western species, or species with very strongly and brightly colored yellow base.

C. Cystidia of recently dried specimens, if treated with formaline, and afterwards mounted in KOH, frequently pinkish, or at least the incrustations of the elements of the hymenium partly or entirely deep pink to purplish red; context of the pileus (subhypodermial

zone) and sometimes strongly in the base of the stipe turning pinkish to red on injury; pileus pale purplish vinaceous to pale grayish vinaceous, or colored in similar cold, pallid hues, pallescent in age .....10. *G. Smithii*

C. Cystidia and incrustations not reacting as described above; context not changing to pinkish or red in any part, or at least not becoming so by autoxydation when exposed to the air; pileus either more salmoneous-testaceous to fawn color, or more distinctly livid-brown, not, or not strongly and constantly, pallescent.

D. Pileus in some combination of pink; the average carpophore medium sized; base whitish or yellow; spores 12–22 × 4.8–6.8 μ, mostly 14.2–18.5 × 5.8–6.8 μ—when taken from a print; mycelium most frequently associated with *Abies* sp. or *Pseudotsuga*, Western species .....11. *G. subroseus*

D. Pileus livid brown, never pink; the average carpophore rather tall and stout; spores 15–24 × 5–7.5 μ, mostly 15.3–20 × 5.2–6.2 μ, *i.e.*, in average slightly longer and narrower than in *G. subroseus* in prints taken from American specimens; species occurring in the East as well as in the West under *Pinus* spp. and *Picea* spp., occasionally also under *Abies* and *Pseudotsuga*.
12. *G. glutinosus*

8. GOMPHIDIUS SEPTENTRIONALIS Singer

Papers Mich. Acad. Sci. Arts and Letters **32**: 149. 1948

Pileus obconic, flat or convex, later more or less depressed, obtuse or subumbonate, 35–40 mm. broad; surface of the viscid pellicle glabrous, smooth, "pale ochraceous salmon" to "light pinkish cinnamon," becoming darker, about "vinaceous cinnamon," the disc somewhat darker, when dried "ochraceous buff" to "cinnamon" (more fuscous if dried too fast and hot, or too slowly); context "pinkish buff" to salmon; lamellae decurrent, subdistant, rather broad, sometimes a few forked, white, becoming pale gray, eventually darker because of the spores; spore print black (or nearly so); spores 15.7–22.5 × 6–8.5 μ, melleous gray, grayish fuscous, or honey-yellow, with thin to thick (0.8 μ) walls, subfusoid to fusoid; basidia (29) 39–52 × 10–13.5 μ, 4-spored, very few 2-spored; cystidia (55) 88–170 × (12.3) 15.7–18.5 μ, rather numerous, hyaline, sordid-pallid, or gray, cylindric or ventricose, with rounded apex, more rarely fusoid; subhymenium filamentous, of hyaline, interwoven hyphae, moderately dense; mediostratum distinct in young specimens, later not very distinct; stipe cylindric, somewhat striate with a narrow dry apical zone which is silky-fibrillose, subconcolorous with the pileus above, or more rarely paler, with a deep brilliant yellow base and with more or less blackened areas or reticulations in some specimens, with an apical membranaceous

annulus consisting of subparallel-interwoven hyaline, nonincrusted hyphae of 2.8–6.2 μ diameter, the extreme apex of the stipe with some dermatocystidia which however do not form fascicles or glands, or sometimes the annulus indistinct or lacking, but then with 1–3 narrow glutinous belts near the apex but never broadly glutinously sheathed in its lower portion, solid, 50–85 × 5–12 mm.; context concolorous with the surface; odor none; taste mild; mycelium yellowish white; veil predominantly fibrillose but viscid on its outer side when covering the hymenophore, well developed; all hyphae without clamp connections.

Type locality: Portapique Beach, Nova Scotia, Wehmeyer, 1769. University of Michigan Herbarium.

Habitat: Under *Picea* and *Abies* among their needles in mixed (spruce-fir-birch) woods, fruiting from August to October, often associated with *Boletinus*.

Distribution: From the Maritime Provinces (New Brunswick and Nova Scotia, Canada) to Maine, U. S. A.

Notes: This and the two following species (9–10) are, of all species of *Myxogomphus*, most closely related to *Laricogomphus*.

9. GOMPHIDIUS NIGRICANS Peck

N. Y. State Mus. Rep. **48**: 12. 1897

Gomphidius vinicolor Peck var. *minor* Kauffman, Agar. Mich. **1**: 171. 1918.

Pileus rather fleshy with very thin margin, hemispheric to convex then repand, at least the disc becoming flattened, the margin at first incurved, (10) 20–70 mm. broad; pellicle very glutinous, very strongly shining when dry or dried, entire or cracking either into small areolae or radiately, thick, separable, in the very early stages white, then more and more "pinkish vinaceous" to flesh color and turning blackish brown or quite black when old or drying; context white or concolorous with the surface in the upper portion and white below; lamellae white then becoming gray and eventually black, subclose to distant, decurrent, some (a variable percentage) forked, easily separating from the context of the pileus; spores (14.3) 15.7–20 × (4.8) 5.5–6.3 (7.2) μ, brownish, sometimes a pure deep slate gray, cylindric to fusoid; basidia 40–52 × 9–12.5 μ, 4-spored, very few occasionally 2-spored, often with a grayish cell-sap; cystidia (67) 73–105 (130) × (8) 13–17 (20) μ, very numerous in most young specimens, very scattered in old ones, thin-walled, cylindric to mostly more or less ventricose or clavate, comparatively short in most specimens, with the projecting tips covered

with a sordid melleous to brown detersible, resinaceous incrusting hood, or a granular melleous incrustation, some (often all) with a deep gray cell-sap; subhymenium slightly denser than in *G. glutinosus,* the elements however of the same structure and shape but often with a grayish cell-sap, usually filamentous; trama showing the same structure as in *G. glutinosus;* stipe whitish, the apex remaining so for a while, the lower portion soon blackening entirely, because of a slimy hyaline coating that covers almost the entire stipe except the apex and causes it to become very shiny when dry, possible occasionally reticulately blackening, the transition from white to black sometimes by intermediate colors like "dark vinaceous," the base itself not covered by an abundant mycelial tomentum and not remaining paler in the blackened specimens, (30) 40–80 × (2) 3–8 mm.; context whitish, eventually sordid blackish, at times somewhat pinkish in the base, not yellow; odor none or slight; taste mild; all hyphae without clamp connections.

Type locality: Westport, N. Y., N. Y. State Mus. (type seen).

Habitat: Under or near pines (*Pinus strobus*), fruiting in August and September.

Distribution: From Massachusetts to North Carolina, and west to Michigan and Tennessee.

Illustration: Atkinson, Stud. N. Am. Fung. fig. 50–51 (?) (see "Doubtful species").

10. GOMPHIDIUS SMITHII Singer

Papers Mich. Acad. Sci. Arts and Letters **32**: 150. 1948

Pileus fleshy, thinner toward the margin, convex with initially incurved margin, 30–60 mm.; surface of the glutinous pellicle glabrous and smooth, "pale purplish vinaceous" to "purplish vinaceous," varying to "pale grayish vinaceous"; context white, soft, becoming very slightly flushed with vinaceous or pink in some caps when cut; with KOH yellowish at first, finally discoloring; with NH_4OH slowly pinkish; with $FeSO_4$ instantaneously blackish in the upper part of the pileus, lamellae decurrent, subclose to subdistant, white then grayish, narrow to moderately broad, frequently forked once or twice, edge even; spore print between "clove brown" and black; spores 15–19.5 × 5.5–6.5 μ, pale melleous to grayish brown, subfusoid to fusoid; basidia 50–60 × 9–12 μ, 4-spored, their apices often covered with a resinaceous incrustation; cystidia 109–160 × 13.5–19 μ, numerous, eventually scattered, hyaline to rarely gray, purplish pink (at least many) in an alkali (15 p.c. KOH) medium if previously treated with formalin, otherwise with mel-

leous granular or scaly incrustation, ventricose or subcylindric; subhymenium and trama of the general type of *G. glutinosus;* stipe slightly enlarged downward and then often tapered almost to a point at the very base, white fibrillose beneath, entire surface whitish and finally sordid vinaceous to blackish when handled, solid within, 50–80 × 8–12 mm.; veil hyaline and glutinous, forming a hyaline, glutinous sheath that covers the lower three quarters of the stipe; context white except for yellow in the extreme base, soon distinctly pinkish in base where cut, reactions as in context of pileus; mycelium between "cream buff" and "cinnamon buff" (when dried); all hyphae without clamp connections.

Type locality: Rhododendron, Ore., A. H. Smith 19312; Univ. Mich. Herb.

Habitat: Scattered under lodgepole pines and Douglas fir.

Distribution: Oregon, U. S. A.

Note: This species, which has the colors of the fresh carpophores as well as the chemical characters including the immediate autoxidation of the context and the purplish cystidia in KOH (quite different from *G. subroseus*), is hardly distinguishable from *G. subroseus* var. *homobasis* when merely compared in the herbarium; the purplish coloration of the cystidia was absent in material of *G. subroseus* and *G. glutinosus* dried in exactly the same way and at the same time.

Var. *xanthobasis* Singer, Papers Mich. Acad. Sci. **32**: 150. 1948. Base of the stipe distinctly bright yellow. Under a plantation of *Pinus flexilis* in the old Harvard Forest, Hamilton, Mass.

11. GOMPHIDIUS SUBROSEUS Kauffman
Mycologia **17**: 120. 1925

Pileus fleshy, abruptly thin at margin, hemispheric or convex to repand, becoming plane or broadly depressed, obtuse, 30–90 (100) mm. broad; surface glabrous, smooth, or sometimes slightly innately striate or very slightly wrinkled under the glutinous or viscid surface layer, shining when dry, "testaceous," "vinaceous fawn" (rarely reaching "fawn color"), "light cinnamon drab," "vinaceous tawny," "flesh color," "vinaceous pink," "ocher red," "Japan rose," "salmon buff," "vinaceous buff," "salmon color," the margin concolorous or paler, becoming "onion skin pink" or "buff pink," the center in old caps reaching "terra cotta" or "cameo brown," or fading to the color of the margin, rarely in young fresh specimens

reaching a color as intense as "carnelian red" or "carrot red" or "light coral red"; margin at first incurved; context white or tinged very slightly with the color of the surface at least near the pellicle; negative with $FeSO_4$ in the main part of the context of the pileus and stipe (probably as in *G. glutinosus*); odor none; taste mild; lamellae decurrent, rather broad (3–8 mm.) at least in medium and large caps, close to subdistant, some forked near the margin and/or near the stipe, whitish to "pale mouse gray" or "pallid neutral gray," then "smoke gray" or "avellaneous" to "wood brown" and eventually speckled darker by the spores which are between "bone brown" and black in a good print; spores 12–22 × 4.8–6.8 μ, mostly 14.2–18.5 × 5.8–6.8 μ when taken from a print, subfusoid-subcylindric, melleous-pallid to grayish brown or gray; basidia 46–63 × 10–12.5 μ, 4-spored, very rarely very few 2-spored; cystidia 65–145 × 9–22 μ, numerous, cylindric or somewhat ventricose, rarely clavate, hyaline with some pale melleous to brownish melleous granular resinous incrustations, thin-walled; subhymenium and trama as in *G. glutinosus;* stipe tapering downward or subequal, curved or straight, glabrous or very slightly fibrillose, white except for the basal 20 or more mm.'s which are "empire yellow," "citron yellow," "amber yellow," "light cadmium" or "apricot yellow," the whole stipe tending to assume black spots, solid, 40–90 × 5–20 mm., veil sometimes forming a viscid, cortinoid but extremely narrow easily gelatinizing annulus from the portion of the veil that joins with the margin of the pileus, otherwise entirely glutinous and hyaline, forming a sheathing covering up to a line close to the very apex of the stipe, which is subpruinose, and unless this slimy coating is washed off by heavy rains the surface remains shiny in dried material; context concolorous with the surface; mycelium often forming a grayish-melleous to grayish stramineous or (away from the yellow base) more pallid grayish-fuscous mycelial tomentum; all hyphae without clamp connections.

Type locality: Mt. Hood, Ore.; University of Michigan Herb. (type seen).

Habitat: On humus and among mosses in coniferous woods and open barrens, probably mostly associated with *Abies, e.g., A. grandis,* possibly also with *Picea, e.g., P. Engelmannii,* or *Pinus, e.g., P. ponderosa,* or *Pseudotsuga taxifolia;* fruiting from June to January (the farther south the later).

Distribution: From British Columbia to Northern California and to Montana and Colorado.

Illustration: Kauffman, Mycologia 17, pl. 13. 1925.

Var. *homobasis* Singer, Pap. Mich. Acad. Sci. **32**: 150. 1948. Base of the stipe little or not colored yellow. With the type.

12. GOMPHIDIUS GLUTINOSUS (Schaeff. ex Fr.) Fries
Epicr. Syst. Myc., p. 319. 1838

Agaricus glutinosus Schaeff. ex. Fr., Syst. Myco. **1**: 315. 1821.
Cortinaria viscida S. F. Gray, Nat. Arr. Brit. Pl. **2**: 629. 1821.

Pileus fleshy, often very thin at margin, pulvinate to convex, then repand, becoming plane or somewhat depressed, obtuse or rarely subumbonate, 50–100 (137) mm.; surface glabrous, smooth, glutinous, shining when dry, "Rood's brown," "Verona brown," "Natal brown," "fawn color," then "walnut brown," "army brown," "pecan brown," or even "sorghum brown," occasionally reaching "carob brown," all these colors often pallescent or diluted with less pigmented spots, eventually often dotted by large "bone brown," or "fuscous" to black areas, reactions with $FeSO_4$, H_2SO_4 on pellicle negative, with NH_3 somewhat lilaceous pink; context white, becoming somewhat sordid in age, or assuming a very slight pinkish hue but unchanging when bruised, soft; odor none or almost none; taste mild or slightly acid; with NH_3 lilaceous pink, with NH_4OH sordid pink; formol in young specimens negative, in old ones slightly reddish after prolonged exposure; $FeSO_4$ negative; H_2SO_4 negative; the infrahypodermial zone with NH_3 distinctly purplish carmin to violet, with $FeSO_4$ greenish black to black, with H_2SO_4 pale brown, with formol quickly reddening; lamellae decurrent, forked, 5–10 mm. broad, subclose to distant, white then pale gray to "smoky gray" and eventually darker because of the spores; spore print between "bone brown" and black; spores 15–24 × 5–7.5 μ, mostly 15.3–20 × 5.2–6.2 μ in prints from American material, fuscous-gray or pale melleous-gray, cylindric-fusoid, with a slight suprahilar depression; basidia 45–55 × 9.5–12.5 μ, 4-spored; cystidia 90–160 × 12–18.5 μ, at first abundant, becoming scattered with age, hyaline or at times some of them with gray contents, subcylindric or somewhat ventricose with rounded apex; subhymenium filamentous or filamentous-cellular (if the septa are close enough), rather dense but looser than in the other sections, hyaline; hymenopodium rather dense, of interwoven hyphae; mediostratum pale melleous and rather dense, of axillar and subparallel hyphae; lateral stratum of subparallel hyphae, as a whole running parallel with the mediostratum, not diverging, looser than the mediostratum and the hymenopodium; stipe either subequal or tapering from the middle downward, often somewhat constricted at the apex, mostly straight, glabrous or very slightly longitudinally fibrillose, white or,

occasionally, becoming pale brownish, or with a very slight pinkish hue, except for the basal 25 or more mm. where it is "empire yellow," "wax yellow," or "primulin yellow," everywhere tending to assume large black spots (not glandular, however), solid, 40–90 × 10–22 mm.; veil sheathing the stipe with a slimy hyaline coating up to a circular annuliform line very close to the lamellae from where in young specimens the hyaline, entirely glutinous veil joins the margin of the pileus, consisting of hyaline, subparallel-subinterwoven, irregularly filamentous and non-incrusted hyphae of 0.8–4.2 μ diameter, imbedded in a glutinous mass; context concolorous with the surface but the white (upper) portion becoming sordid from the middle of the stipe outward, and then in the sordid portion reacting with $FeSO_4$ to greenish gray to black, otherwise reacting as in the pileus, the yellow (lower) portion however with $FeSO_4$ golden-yellow-subferruginous; all hyphae without clamp connections.

Type locality: Regensburg, Bavaria (no type specimens in existence).

Habitat: Among needles, grasses, mosses, in not too dense coniferous or mixed woods, the mycelium connected with mycorrhiza, preferably of spruce (*Picea* spp.) but also other coniferous trees (*Pinus*, possibly *Abies*, *Pseudotsuga*, *Tsuga*), fruiting from July to November, most commonly from August to October.

Distribution: Canada and United States (Northern States and some of the Southern States in mountainous regions), from the Atlantic to the Pacific Coast; also in Europe.

Illustrations: Bresadola, Icon. 671; Ricken, Blätterp. 2, pl. 3, fig. 1; Schaeffer, Bav. 4, pl. 36; Gramberg, pl. 9; Michael, pl. 32; Maublanc 1: 132 II; Cooke, Illustr. pl. 856 (879); Kauffman, Mycologia 17, pl. 12 (could also be *G. subroseus*); see also Saccardo, Syll. **19**: 788. 1910.

Exsiccata: Herpell, Samml. praep. Hutp. 33, 89; Fuckel, Fung. Rhen. 1428; Petrak, Fl. Bon. Mor. 2164; Clements, Crypt. Form. Colo. 360; (*G. viscidus*); Saccardo, Mycol. Ital. 210.

Forma *maculosus* Quél. (ut var.), Flor. Mycol. p. 112. 1888. This is the white form (pileus white, not livid brown), occurring with the type form.

Note: The European and some of the eastern collections in this country have larger spores than the mid-western and western collections, which in many regards gradually become more and more

Photo A. H. Smith.

FIG. 3. *Gomphidius oregonensis*. ×1.

similar to *G. subroseus* as they enter the area of this species. This intergradation may even occur occasionally in size and shape. Consequently, it is not always easy to distinguish western collections of this species from *G. subroseus* without complete data on the fresh plant.

Section *Microsporus* Singer
Papers Mich. Acad. Sci. Arts and Letters **32**: 149. 1948

13. GOMPHIDIUS OREGONENSIS Peck (FIG. 3)
Bull. Torr. Cl. **25**: 326. 1898

Pileus fleshy, abruptly thin at margin, convex to expanded, becoming plane or slightly depressed, obtuse, 30–70 (100) mm.; surface glabrous, with a thick viscid to glutinous surface layer, "wood brown," "avellaneous," or with a flesh color hue, often black-spotted; margin incurved; context white, or with a slight pinkish hue; with KOH yellowish; with NH_4OH and NH_3 pinkish; with $FeSO_4$ instantaneously inky; odor none; taste mild; lamellae subdecurrent, close to subdistant, rather narrow, some or many forked, whitish becoming gray; spore print between "bone brown" and black; spores 11.5–14 (16) × 4.8–5.8 μ, melleous-gray to beautifully pure gray, cylindric to ellipsoid-subfusoid; basidia 40 × 9–10 μ, 4-spored; cystidia 90–125 × 8–12 (21) μ, thin-walled, with a fulvous-castaneous incrusting resinaceous hood, or with granular melleous incrustating fragments, hyaline to grayish, sometimes some with a purplish tinge in formal-KOH, cylindric or slightly ventricose, scattered to numerous; subhymenium filamentous, rather loose; hymenopodium dense and irregular, consisting of hyphae which project in all directions; mediostratum and the hymenopodium consisting of subparallel hyphae; stipe sometimes cespitose, subequal to subventricose, with tapering base curved or straight, glabrous to fibrillose, white above, bright lemon yellow below, tending to become blackish at places where handled or in age, or on drying, solid, (25) 60–110 × (5) 10–28 mm.; veil sheathing the stipe, like it does in *G. glutinosus*, up to the apical annuliform zone from which in young specimens a hyaline, glutinous veil extends to the margin of the pileus; mycelium often forming a tomentum at the base, bright yellow; context concolorous with the surface; all hyphae without clamp connections.

Type locality: Oregon, N. Y. State Mus. (type seen).

Habitat: Under *Pseudotsuga* and *Abies*, on the ground, fruiting from September to December.

Distribution: From Washington to California.

Note: Among the species of section Macrosporus this seems to be closest to *G. Smithii.* It grows plentifully and is edible as are all Gomphidii.

DOUBTFUL AND EXCLUDED SPECIES

Gomphidius roseus (Fr.) Karst. sensu aut. amer. The European species stands out because of its outwardly viscid but not entirely glutinous veil which would make it key out with *G. septentrionalis,* its constant association with *Pinus silvestris* and *Suillus bovinus* (L. ex Fr.) O. Kuntze, its rosy pileus ("light coral red" to "coral pink" at places reaching "carrot red," and margin near "pale flesh color" or "pale salmon color," or entirely in the latter colors), which makes it comparable with the American pink species, and the characteristic habit (short stipe, tapering downward to a slightly warm yellow or more often pink base). The spores are of the size found in section Macrosporus, viz. 17.3–24 × 5.8–7.5 μ; basidia 60–70 × 9–10.8 μ, 4-spored; cystidia 100–120 × 11.6–17.5 μ, rather numerous, little or not incrusted, cylindric or cylindric-ventricose, hyaline; subhymenium and trama as in *G. oregonensis;* chemical reactions similar to those of *G. glutinosus* but the base of the stipe reacting the same way as the infrahypodermial zone. The American authors mentioning *G. roseus* have not seen the real *G. roseus* but one of the American pink species, *i.e., G. septentrionalis, G. Smithii, G. nigricans, G. subroseus* (especially var. *homobasis*) and perhaps *G. oregonensis.*

Gomphidius stillatus Strauss in Sturm, Deutschl. Flora III, **33–34**: 3. 1853. The Bavarian type's position is somewhat doubtful though the European authors now generally agree that it is a form of *G. maculatus.* There is also a chance that it might be *G. glutinosus* f. *maculans. G. stillatus* has been cited by American authors as occurring in this country but here we have almost certainly either one of the above-mentioned forms or a young white stage of *G. nigricans.*

Gomphidius nigricans Peck sensu Atk., Mushrooms, p. 49. 1900. This is a stouter plant than the species described by Peck. We have not seen the latter vary as much as to include Atkinson's

conception as represented in his photographs although we do not exclude this possibility.

Gomphidius rhodoxanthus (Schw.) Sacc., Syll. **5**: 1139. 1887. This is not a *Gomphidius* but *Phylloporus rhodoxanthus* (Schw.) Bres. under which name it has been treated in North American Flora 10 (3); 193. 1917.

Gomphidius foliiporus Murr., Mycologia **35**: 432. 1943. This is not a *Gomphidius* but *Phylloporus rhodoxanthus* (Schw.) Bres. ssp. *foliiporus* (Murr.) Sing., Farlowia **2**: 280. 1945.

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NOTES AND BRIEF ARTICLES

Three New Fleshy Fungi

Amanitopsis floridana sp. nov. Pileo plano, 5 cm. lato, avellaneo, striato, grato; lamellis liberis, albis, confertis; sporis ellipsoideis, levibus, 11–13 × 6–7 μ; stipite albo, glabro, clavato, 4 × 0.5–1.5 cm.; volva ampla, pallida, lobata, glabra, 2.5 × 2.5 cm.; volvella parva, alba, 5 mm. alta.

Pileus plane, 5 cm. broad, dull, glabrous, slightly viscid when wet, avellaneous with blackish disk, center smooth, margin closely striate for fully 1 cm., straight, fertile, entire, subconcolorous; context very thin, white, unchanging, odorless, mild; lamellae ventricose, crowded, inserted, milk-white, unchanging, free, abruptly depressed behind, about 7 mm. broad, entire; spores ellipsoid, smooth, uniguttulate, 11–13 × 6–7 μ; stipe inverted, peg-shaped, smooth, glabrous, white, unchanging, 4 × 0.5 – 1.5 cm., outer volva tough, not friable, ample, dirty-white, with three broad, acute lobes, glabrous, white inside, 2.5 × 2.5 cm.; inner volva (volvella) thin, white, about 5 mm. high, slightly lobed, closely encircling the base of the stipe like a collar.

Type collected by W. A. Murrill in rich soil at the base of a loblolly pine in a grove of frondose trees in Gainesville, Fla., August 5, 1948 (*F 21484*). This species looks like a combination of two, the cap greatly resembling that of *A. vaginata* and the volva suggesting that of *A. volvata* or *Amanita porphyria*. The spores, however, are not globose as in *A. vaginata* but ellipsoid like those of *A. strangulata*, which has a friable volva colored mouse-gray on the inside instead of white. To complicate matters still further, it is the tawny form of *A. vaginata*, not the gray, that has the secondary volva, a feature known also in *Amanita Caesarea* but not figured by Bresadola in his plate of that species. In my nomenclature this interesting addition to our flora would be *Vaginata floridana*.

Volvaria flaviceps sp. nov. Pileo campanulato, 3.5 cm. lato, flavo, fibrilloso; lamellis liberis, latis, albis, sterilibus; stipite albo, glabro, 4 × 0.6–1 cm.; volva ampla, 4 × 2.5 cm., subumbrina, squamosa.

Pileus campanulate, solitary, 3.5 cm. broad; surface dry, smooth, fibrillose, uniformly bright-flavous, margin fimbriate, projecting 2

mm.; context very thin, white, unchanging, with a peculiar sickening odor during drying; lamellae free, broad, wide and rounded at the margin, narrow behind, crowded, very thin, entire, white, unchanging, sterile; stipe smooth, white, glabrous, curved, enlarging below, 4 × 0.6–1 cm. above the volva, which is 4 cm. high and 2.5 cm. broad at the top, tapering to 1 cm. at the base, dry, dirty-white with large, flat, pale-umbrinous scales, their acute tips pointed upward.

Type collected by W. A. Murrill on the underside of a shaded magnolia log in Gainesville, Fla., July 11, 1948 (*F 22458*). A very rare, noteworthy, and beautiful species closely resembling *V. bombycina* in form and habit but with bright-yellow cap and scaly volva.

Boletus flocculosipes sp. nov. Pileo convexo-expanso, 9–14 cm. lato, fuligineo, imbricato-floccoso, grato; tubulis 1 cm. longis, 1–2 per mm., flavis, olivascentibus; sporis ellipsoideis, striatis, olivaceis, 12–14 × 6–7 μ; stipite floccoso, rubro-brunneo, 6 × 2–2.5 cm.

Pileus convex to expanded, gregarious, 9–14 cm. broad; surface coarsely shaggy, fuliginous, margin concolorous, entire, fertile, incurved when young, with no trace of a veil; context pale-yellow, pinkish near the surface, bright-blue at once when cut, 1–2 cm. thick, odorless, mild; hymenium plane to somewhat ventricose, not depressed at the stipe, sulphur-yellow to dirty-sulphur and finally brownish, dark-blue-green at once when bruised; tubes 1 cm. long, 1–2 per mm., angular, not stuffed, inside same as mouths in color and change of color, taste mild; spores suggesting a long watermelon, oblong-ellipsoid, deep-olive-green when fresh, conspicuously longitudinally striate, uniguttulate, 12–14 × 6–7 μ; stipe subequal, solid, 6 × 2–2.5 cm., hispid-shaggy, reddish-brown, yellow and glabrous at the apex, fuliginous at the base, bright-yellow inside, turning greenish-blue at once when cut.

Type collected by W. A. Murrill in bare soil near *Carya magnifloridana* Murr. in Gainesville, Fla., Aug. 7, 1948 (*F 39840*). Strongly suggesting *Strobilomyces* in the covering of cap and stem but not otherwise. In some ways it is rather close to *Frostiella* but that does not seem to be the natural place for it.—W. A. MURRILL.

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